MACROFAUNAL COMMUNITY STRUCTURE ON THE GULF OF MEXICO CONTINENTAL SLOPE: THE ROLE OF DISTURBANCE AND HABITAT HETEROGENEITY AT LOCAL AND REGIONAL SCALES

A Dissertation

by

ARCHIE WOOD AMMONS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2007

Major Subject: Zoology

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Approved by:

Co-Chairs of Committee,	Mary Wicksten
	Gilbert Rowe
Committee Members,	Duncan MacKenzie
	Lisa Campbell
Head of Department,	Vincent Cassone

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ABSTRACT

Macrofaunal Community Structure on the Gulf of Mexico Continental Slope: The Role of Disturbance and Habitat Heterogeneity at Local and Regional Scales. (May 2007)

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Co-Chairs of Advisory Committee: Dr. Mary Wicksten
Dr. Gilbert Rowe

The ecological forces that drive community structure of deep-sea benthic communities are poorly understood, yet such communities rival in biological complexity those of coral reefs or rainforests. Using components of the recently concluded DGoMB project, local and regional-scale structure of benthic macrofaunal communities were examined at thirty two locations throughout the continental slope of the northern Gulf of Mexico. Controlling factors associated with sediment disturbance, food supply, and faunal competition between functional ecological groups were evaluated for correlative and relational patterns. A higher order taxonomic sufficiency approach was used to calculate both alpha and beta diversity.

The results of this study indicate that macrofaunal communities are very patchy, having wide variations in abundance at within-site, adjacent-site, and across-basin scales, yet all sample areas possess a large richness of higher taxa. Declining abundance was noted with increasing water depth and reduced particulate organic carbon levels. Upper-slope submarine canyons possess some of the highest abundances. Less mobile macrofauna, such as poriferans, bivalves, and scaphopods, dominate slope communities

above the 500 meter contour. Sediments exhibiting intense megafaunal bioturbation inhibit abundances of sedentary macrofaunal taxa, but such mixing is positively associated with increased abundances of polychaetes and ambulatory crustaceans, including peracarids, harpacticoids, and ostracods. Prominent sediment mixing was noted at most sites, including portions of the Sigsbee Abyssal Plain. The western Gulf of Mexico was less biologically active than the eastern Gulf of Mexico, which possesses two extensive submarine canyons that appear to act as regional nutrient traps. I conclude that the physiographic complexity of the northern Gulf of Mexico continental slope influences macrofaunal community structure. Biological disturbance, in the form of sediment mixing, is widespread throughout most slope depths, and the benthic environment is food-limited. It appears that disequilibrium-type ecological processes predominate in this area, supporting similar findings by previous studies in other regions of the ocean, usually at far smaller scales and none representative at the basin-level. Use of higher order taxonomy in lieu of genus or species-level faunal identifications for diversity measurements was inadequate for detecting spatial patterns or environmental responses.

DEDICATION

To Fain Hubbard

ACKNOWLEDGEMENTS

This study could not have been accomplished without the support and assistance of the many individuals involved with the DGoMB project. Primary thanks are due to chief scientist Dr. Gilbert Rowe, who oversaw the entire program, and Dr. Fain Hubbard and members of the benthic ecology laboratory, for performing the extremely time consuming and labor-intensive task of separating and identifying over 100,000 macrofaunal organisms. Thanks are also due to the crew and support personnel of the oceanographic research ship RV *Gyre*, as well as the various project scientists, their technicians and graduate students that collected the various biological, physical and chemical data used in this study. Dr. Mary Wicksten provided numerous insights into the behavior and ecology of both macrofaunal and megafaunal invertebrates. Matt Ziegler operated the benthic camera system and compiled all of the seafloor photographs. Sophie DeBeukelaer instructed on the use of GIS software and supplied map templates for the study area. Undergraduate research students Kelly Davis and Amanda Keith evaluated over 1,000 seafloor photographs for bioturbation. The statistical design of this project was heavily influenced by Dr. Jay Pinckney's outstanding graduate biostatistics course. Dissertation drafts were extensively reviewed by Dr. Lisa Campbell and Dr. Duncan MacKenzie. Final thanks are due to the Mineral Management Service, who provided the funding for the DGoMB project (# 30992).

TABLE OF CONTENTS

LIST OF FIGURES

FIGURE Page

FIGURE Page

FIGURE Page

FIGURE Page

LIST OF TABLES

TABLE Page

1. INTRODUCTION

In terms of sheer area, the marine realm is the largest on the Earth. The vast bulk of this area comprises two distinct ecological zones, the pelagic and the soft deep-sea bottom. Due to the expense and logistical support necessary to conduct deep-sea studies, it is poorly known. Indeed, out of roughly 270 million km^2 of the deep sea floor, only about 500 m^2 has been quantitatively sampled from cores (Gage, 1997).

This is unfortunate, for the studies that have been done since the 1960's indicate a much more complex and dynamic system than was historically thought (Sanders, 1968). Until this time, it was long believed that the deep-sea was species depauperate. Marshall (1954) summarized the scientific opinion of the time in stating, "with increasing distance from the land there is increasing tendency for the deep-sea floor to be populated by fewer individuals belonging to fewer species". Hessler and Sanders (1967), using the newly created epibenthic sled, refuted this statement when their analysis revealed species diversity rivaling that of the shallow marine tropics. Since that time, most studies have supported Hessler and Sander's work. It is currently well known that in terms of *number of species*, the deep sea is rivaled only by tropical rainforests and hermatypic reefs. However, the deep sea is so fundamentally different (and much more poorly studied) from these other communities that the last thirty-odd years have focused on diversity-driving theory (that is, forces that create and maintain diversity). These have generally fallen into two categories (Table 1).

This dissertation follows the style of Deep Sea Research II.

Table 1
Common diversity theories applied to the deep sea. Adapted from Gage and Tyler, 1991.

Equilibrium Processes:	**Disequilibrium Processes:**
•species highly specialize/coexist via habitat and/or resource partitioning •communities operate at/near carrying capacities •competitive exclusion minimized due to extreme species specialization	•local or widespread disturbances keep populations below carrying capacity •competitive exclusion inhibited by environmental and/or biological disturbances that keep populations in early growth phase
1. Stability-Time (Sanders, 1968; Slobodkin and Sanders, 1969; Grassle and Sanders, 1973) •physical stability in deep-sea allows extreme species specialization on *evolutionary time scale*	**1. Biological Disturbance** (Dayton and Hessler, 1972) •effects of large feeding predators/croppers cause sufficient disturbance to: ➢ depress competitor abundance ➢ keep resources from becoming limiting ➢ reduce competitive interactions (reducing trophic interaction and maintaining generalist diets)
2. Trophic Partitioning (Valentine, 1973) •*decreased* <u>food</u> availability drives speciation	
3. Habitat Heterogeneity (Jumars, 1975; Etter and Grassle, 1992) •*increased* <u>spatial</u> variability drives speciation •deep-sea spatial variability mostly small-scale, maintained by high sediment stability	**2. Intermediate Disturbance** (Connell, 1978; Grassle and Maciolek, 1992; Kukert and Smith, 1992) •diversity maintained via infrequent disturbance events (physical or biological) •stability periods allow new species immigration and resource partitioning •disturbance periods disrupt competitive exclusion

Equilibrium processes emphasize habitat stability, at both the local and regional scale. Regionally (i.e. basin-wide), remarkably static physical (sediment type, temperature) and chemical (salinity, pH, dissolved oxygen) deep-sea features support Sanders' (1968) *stability-time theory*. On evolutionary time scales, constancy of environmental variables

should allow biological interactions (competition, predation, specialization), and thus speciation to be favored. Further refinements by Valentine (1973) incorporated *trophic partitioning* concepts, whereby high diversities relate to food resource stability. Valentine argues that the deep sea, being both oligotrophic and trophically static, would allow resource carrying capacities to be easily reached (due to its oligotrophy) and maintained (via static nutrient inputs). This would force organisms into increasingly specialized feeding niches, in order to exclude competitors. Such systems are characteristic of tropical coral reefs and rainforests, where many of the resident biota possess highly distinctive feeding strategies.

At smaller, local scales, persistence of sediment features favors the *habitat heterogeneity theory*. Explored primarily by Jumars (1975), Jumars and Eckman (1983) and Thistle (1983), the theory heavily borrows from niche partitioning ideologies for tropical rainforests and coral reefs. In such cases diversity is hypothetically fueled through exploitation of numerous micro-habitats created by biogenic activity; the rainforests' multi-leveled tree canopy and the coral reefs' bioherm complex would provide these micro-habitats. Much of the deep sea is postulated to similarly contain high structural complexity, in the form of burrows, mounds, faecal casts, and tracks. These "lebensspuren" (life traces), unlike their shallow water counterparts, are not quickly removed by physical disturbance, but persist for long periods of time. For macrofaunal and smaller size classes, deep-sea lebensspuren would provide suitable micro-habitats to flee from predators, competitors, and local extinctions (Gage and Tyler, 1991). All of these would serve to maintain *existing* diversity. Creation of new

species however, would come about through either specialization (an equilibrium process) or disturbance (disequilibrium).

The heart of equilibrium theory is the view that communities must remain at carrying capacities (i.e. a climax community). Without this, species are not inclined to deplete food resources and thus be forced into niche specializations. If food resources are *not* limiting in a deep-sea habitat, then disequilibrium theory comes into effect.

Disequilibrium processes assume that communities never reach carrying capacity, and stress habitat *in*stability. Such instabilities are caused by disturbances, either biologically or physically mediated. Disequilibrium theories (also known as dynamic or non-equilibrium hypotheses) arose to help explain diversity peaks on the continental *slope*, which conflict with the nutrient/bathymetric diversity increases postulated for equilibrium processes (Gage and Tyler, 1991).

Biologic disturbance theory in the deep sea was first proposed by Dayton and Hessler (1972). They argue that intense predation depresses prey abundances, and therefore competition between prey species. This would retard competitive exclusion effects and enhance diversity. It would also foster faunas with *non-specialized* feeding lifestyles. Grassle and Sanders (1973) countered that high predation effects would maintain prey faunas in underdeveloped, juvenile stages, or faunas of short lifespan and high reproductive output. It has proved difficult finding communities meeting these latter criteria except under unusual situations (Thistle, 1983) however, and the few studies of deep-sea animal life histories typically support their being long-lived, slow growing, and reproducing little with small clutch sizes (Turekian et al., 1975; Jumars and Eckman,

1983; Gage and Tyler, 1991) The first truly quantitative macrofaunal sampling program (Hessler and Jumars, 1974) did not argue this point, but did show that the majority of organisms were in fact generalist deposit feeders. If and how biologic disturbance theory operates is still, even today a matter of debate.

The *intermediate disturbance hypothesis* (Connell, 1978) offers to solve many of the problems associated with biological disturbance, by incorporating later ideas gleaned from studies on tropical rainforests and coral reefs (much like habitat heterogeneity theory). Connell noted that in these habitats, highest diversity was encountered where *periodic* disturbance took place. Such disturbances could either be biologic (predation) or environmental (storms) in origin. The deep-sea equivalents of these would be megafaunal deposit feeding, benthic storms, sediment slumps, deadfall, and bioturbation. Disturbance events are characterized by Osman and Whitlatch (1978) as having two components, frequency and magnitude. Intermediate disturbance events would ideally be either high frequency or low magnitude (deposit feeding, bioturbation), or low frequency and high magnitude (storms, slumps, deadfall). High diversity comes about through a sequence of events following disturbance. First, opportunists colonize. These are followed by an increasing diversity of species. As the community begins to reach carrying capacity, diversity peaks. A new disturbance event soon follows. If too much time passes without disturbance, resources will become limited and competitive exclusion will occur. This will reduce diversity. If communities are perturbed too often, their diversity will remain low (relegated to opportunists). This is what is thought to occur on the continental shelf, where predation and physical disturbance are more

prevalent. The abyssal plain, on the other hand, does not possess *enough* disturbance; climax communities of no more than moderate diversity result.

The vast size of the deep sea further permits one additional feature of high species diversity, namely the retention of rare species. By definition, having a high species diversity necessitates most species to be rare. However, gene lines that would be naturally extirpated in "normal-sized" habitats could conceivably carry on in the deep sea simply by being too difficult to completely eradicate (Abele and Walters, 1979). Habitat heterogeneity and disturbance theories would enhance this by reducing predation effects, either by reducing predators directly (disturbance), or permitting micro-habitat refuges (habitat heterogeneity). Pineda (1993) tested the effects of range size along bathymetric gradients, and found higher diversities where the gradients were less pronounced (equivalent to greater geographic area).

1.1. Status of the Question

Throughout the 1970's there was great experimentation with deep-sea biological sampling gear and benthic sample processing techniques. In particular, the use of sediment boxcores became prevalent for community analysis at the macro- and meiofaunal size classes. During the 1980's several ambitious sampling programs were undertaken in the northwestern Atlantic, eastern Pacific, and northern Gulf of Mexico. The most notable of these, the Western North Atlantic Continental Slope and Rise Study, covered a 176 km transect and comprised over 200 large ship-deployed boxcores. Grassle and Maciolek (1992) reported 798 species from 21 m^2 of bottom (233 boxcores);

58% were new to science. In the Gulf of Mexico, work comprised NGOMCSS, the Northern Gulf of Mexico Continental Slope Study (Gallaway, Martin and Howard, 1988) and the more recent Deepwater Program: Northern Gulf of Mexico Continental Slope Habitats and Benthic Ecology (DGOMB) study.

Deep-sea species diversity appears to be highest among the macrofauna size-class (animals >0.5-2.0mm), although admittedly the bulk of quantitative data has come from this group, and future taxonomic work might well prove otherwise. Limitations on sampling effort have for the most part restricted macrofaunal sample sizes to less than a square meter of seafloor, woefully inadequate for completely measuring anything other than local diversity. Major difficulties lie in using these samples to categorize larger (typically *much* larger) areas, and differentiating habitat borders.

For the vast bulk of bottom photography, the sampling area appears surficially homogeneous. The bottom is primarily soft, with few identifiable features. Macrofauna are too small to be identified; larger megafauna are typically rare and/or buried. This can easily lead to an impression that an ocean bottom habitat is a massive, basin-wide affair. Early sampling efforts with crude methods and equipment supported this (Dayton and Hessler, 1972). One would assume that if between-habitat variations in diversity occur, it is on the large scale and mediated by environmental factors such as depth and/or sediment type. The problem with this viewpoint is twofold. First, many seabeds display in fact a great deal of structural heterogeneity, but it is often at *very small (decimeter or less) scales* (Heezen and Hollister, 1971). Second, diversity analysis of macrofaunal samples has inherently shown a high percentage of species that differ dramatically from

sample to sample, even when taken at the *same time* within the *same area* (Galloway, Martin and Howard, 1988; Grassle and Maciolek, 1992*)*. Much of this variation is due to extreme rarity of species (many of which are only encountered once), or may be simply stochastic (Osman and Whitlach 1978; Jumars and Eckman 1983). It is also possible that small-scale, microhabitat patches cause this variation. Such "patch dynamics" studies have been undertaken since the mid-1970's (Jumars, 1975), and are still intensely researched (Snelgrove, Grassle and Petrecca, 1996; Rex, Etter and Stuart, 1997; Soltwedel, Queric and Vopel, 2002). The majority of these projects have dealt with the identification, age, and measurements of size and makeup of microhabitat patches. Fewer however have applied this knowledge to large-scale (i.e. regional or basin-wide) diversity patterns (Grassle and Maciolek, 1992, Levin et al. 2001). This is a problem for ecologists. Species flux between adjacent habitats can be an important diversity-driving force in terrestrial and shallow-water systems. Integrating larger scale diversity factors (i.e. sediment type, physiography, storms) with smaller scale ones (bioturbation, deadfall) may better establish their true significance to deep-sea ecosystem structure.

The current study will add to current efforts in multi-scale biodiversity research. Such studies are few and primarily relegated to the western North Atlantic (Levin et al., 2001); the current work will focus within the more structurally complex Gulf of Mexico. In particular, biological and environmental factors causing or contributing to diversity patterns will be explored, at both local and regional scales. This is highly relevant to our understanding of deep-sea ecology.

The Gulf of Mexico is ideally suited for multi-scale studies, due to it possessing a highly variable physiography within a relatively small area. Although formally described as both a regional Mediterranean-type sea (Garrison and Martin, 1973) and small oceanic basin (Uchupi, 1975), the latter designation is more appropriate for ecological purposes. It possesses three of the four major depth zones (the exception being the hadal trenches), as well as canyons, escarpments, basins, abyssal plains, chemosynthetic communities, and extensive salt/shale diapir fields. Pequegnat (1983) and Pequegnat, Gallaway and Pequegnat (1990) describe these features in detail.

The advantage of having a wide variety of physiographic features is that they can be tested as *large-scale* factors affecting diversity. As previously mentioned, few research studies have attempted this (other than bathymetric comparisons). For the most part, relevant work has dealt with seafloor habitats that are either swept with high current regimes (Gage, 1997) or high nutrient flux (Vetter and Dayton, 1998). Submarine canyon systems are the preferred study sites in both of these cases. Little/no work has been done on the role of other distinct physiographic features (i.e. basins, escarpments) on diversity, nor has a submarine canyon as large and active as the Mississippi Canyon (present within the proposed study) ever been quantitatively sampled.

1.2. Testing Diversity-Driving Forces in the Deep Gulf of Mexico

The objectives of this study were to examine differences in macrofaunal community structure at both local and regional scales within the deep Gulf of Mexico, and attempt to determine controlling factors. Central questions cover:

1.2.1. Small-Scale (local) Macrofaunal Patterns

A. How much macrofaunal variation is present within Gulf of Mexico sampling replicates? This was done by identifying and measuring microhabitat patchiness within a sample site.

B. Is the bottom biologically homogeneous between comparison replicates? Faunal differences were delineated between local (within a sample area) and landscape (similar and/or adjacent sample areas) systems.

1.2.2. Large-Scale (regional) Macrofaunal Patterns

A. Do different areas of the Gulf of Mexico produce different amounts of variation? Comparisons were made of faunas from different physiographic types (i.e. canyons, basins), depths, and geographic location (eastern Gulf, western Gulf).

B. What factors correlate with this variation? Comparisons were made against physical (depth, sediment type, POC) and biological (bioturbation intensity) measurements between sampling stations.

1.2.3. Hypothesis

Macrobenthic communities are very patchy. Thus there should be significant variation in macrobenthic diversity, abundance, and feeding/motility "guild" type between boxcore replicates and stations. Following disequlibrium theory, greatest variation should occur in areas of:

- High biogenic activity (visible as "lebensspuren")
- Frequent or pulsed nutrient imports (i.e. detritus-funneling in canyons, shallower water depths)

Null Hypothesis: Macrobenthic communities are homogeneous and there is no significant difference in macrofaunal community structure, either between local-scale boxcore replicates or regional-scale survey stations. There is no relationship between biologically mediated disturbance and community structure within the sampling areas.

2. METHODS

All analyses are derived from data taken from the Deepwater Program: Northern Gulf of Mexico Continental Slope Habitats and Benthic Ecology (DGoMB) project. Field data from this program were collected between the years 2000-2002.

Other than the Northern Gulf Of Mexico: Continental Shelf/Slope Study (NGOMCSS) of the 1980's, the DGoMB project is the only other large-scale, multidisciplinary survey of its kind performed in the Gulf of Mexico. It comprised a wide variety of physical (i.e. temperature, sediment type), chemical (salinity, DO, carbon forms), and biological (photography, trawling, coring) measurements. Earlier large-scale survey expeditions (i.e. *Alaminos*, *Oregon* series) in the Gulf of Mexico were predominantly focused on megafaunal collections.

2.1. DGOMB Research Cruises

Under a U.S. Minerals Management Service contract, the DGoMB project was designed to better understand the biological communities living within/atop the sediments of the northern Gulf of Mexico continental slope. The earlier NGOMCSS project focused much of its efforts on (relatively) confined areas in the Gulf of Mexico, and de-emphasized surveys of the middle and lower continental slope. A much more basin and depth-comprehensive sampling regime was designed for DGoMB. Over three dozen survey stations, ranging from outer shelf to abyssal plain depths, were widely dispersed throughout much of the northern Gulf of Mexico (Fig.1).

Fig. 1. Sample stations for DGoMB (cruise I, May-June 2000), illustrating the large geographic scale of the project. Each dot represents a single community structure survey station, comprising multiple sediment boxcores, bottom photography, and single trawl, in addition to various physical and chemical measurements. 32 of these stations were used for diversity-process testing. Stations indicated in red did not meet all test criteria and were omitted from study.

Many DGoMB survey stations were specifically sited to sample regional areas possessing distinct physiographic properties. The most prominent physiographic regions are listed in Table 2.

Table 2
DGoMB survey areas located within prominent physiographic regions.

Submarine Canyons
Mississippi Canyon (MT-series stations)
DeSoto Canyon (S35, S36, S37-series)
Alaminos Canyon (station AC1)
Escarpments
West Florida Escarpment (S38-S44-series)
Basins
B-series stations (B1, B2, B3)

2.1.1. DGoMB Data Used in This Study

The primary purpose of this study was to measure variation in macrofaunal community structure, and explore patterns supporting equilibrium and disequilibrium-based diversity theory. As such, only DGoMB sampling data viewed pertinent to this was used (Table 3), from survey stations with complete sets of data (Table 4). Excepting photographic analysis of four abyssal plain sites (DGoMB expedition 3B, August 2002), all data were derived from DGoMB expedition I (May-June 2000) field collections and measurements aboard RV *Gyre*. Particulate organic carbon (POC) was sampled from bottom water collected from a single CTD cast taken at each survey station. Sediment grain size fractions and total organic carbon (TOC) percentages were determined from single boxcore samples taken at every survey station. Detailed methodologies for sediment grain size are described by Morse and Beasley (in review), and for all three measurements in the DGoMB program report (Rowe, in review). Sediment total organic

carbon was incorporated into the study at a later date for purposes of cross-comparisons against a related measurement (bottom-water particulate organic carbon).

Table 3
DGoMB sampling measurements used in this study.

Measurements	Purpose in this Study
Water Depth	Habitat selection, indirect trophic indicator
Sediment Grain Size	Habitat selection, specialization
Bottom-water Particulate Organic Carbon	Trophic indicator
Sediment % Total Organic Carbon*	Trophic indicator *
Benthic Photography	Habitat disturbance, megafaunal grazing
Benthic Macrofauna	Community structure

* secondary carbon measurement added later to compare against bottom-water POC

Table 4
List of DGoMB I survey stations.

Complete Data (used)	**Incomplete Data (not used)**
Far NW GoM (94^{o}-96^{0}W) Depth Transect Series: RW1, RW2, RW3, RW4, RW5 Deep Canyon: AC1	Far NW GoM (94^{o}-96^{0}W) Depth Transect Series: RW6
Western & West-Central GoM (91^{o}-94^{o}W) Depth Transect Series: W1, W3, W5, W6 Basins: B1, B2, B3 *Non*-Basins: NB2, NB3, NB5 Other: WC12	Western & West-Central GoM (91^{o}-94^{o}W) Depth Transect Series: W2, W4, *Non*-Basins: NB4 Other: WC5
Central GoM (88^{o}-91^{o}W) Depth Transect Series: C1, C4, C7, C12 Canyon Transect: MT3, MT4, MT5, MT6	Central GoM (88^{o}-91^{o}W) Depth Transect Series: C14 Canyon Transect: MT1, MT2
Far NE GoM (85^{o}-88^{o}W) Escarpment Transect: S41, S42, S43, S44 Canyon Transect: S35, S36, S37	Far NE GoM (85^{o}-88^{o}W) Escarpment Transect: S39, S40 Other: S38

Thirty two of the forty three DGoMB I survey stations contained complete and/or reliable datasets for all of the test measurements in Table 3. The single exception to this was the later-added total organic carbon, which lacked a measurement value at station MT6 (lower Mississippi Canyon). As such, TOC was only examined at 31 DGoMB stations. Survey stations rejected for analysis in this study contained missing and/or questionable data that precluded their use.

2.1.2. Benthic Photography

DGoMB bottom photographs were taken with a BENTHOS DSC 4000 digital still camera deployed from the surface and attached to a shipboard winch (Fig. 2). The camera system was triggered by a magnetic switch, activated by release of tension from a 15 cm weighted line beneath the camera mount. Shipboard winch operators “bounced” the camera system off the seafloor along a specified transect at each survey station. The technique yielded bottom photographs of roughly 2 m^2, typically at 1.5-2.5 minute intervals. Between 1-45 (average: 28) usable photographs were taken at each camera survey station (Fig. 3). Detailed information for the DGoMB camera system is described by Ziegler (2002).

Fig. 2. DGoMB remote camera system, deployed from RV *Gyre*.

Fig. 3. Typical bottom photograph taken with the DGoMB remote camera system. Areal coverage is roughly 2 m^2. The central foreground shows overexposure from the strobe. This is recorded image #29 from survey station S35 within the upper DeSoto submarine canyon.

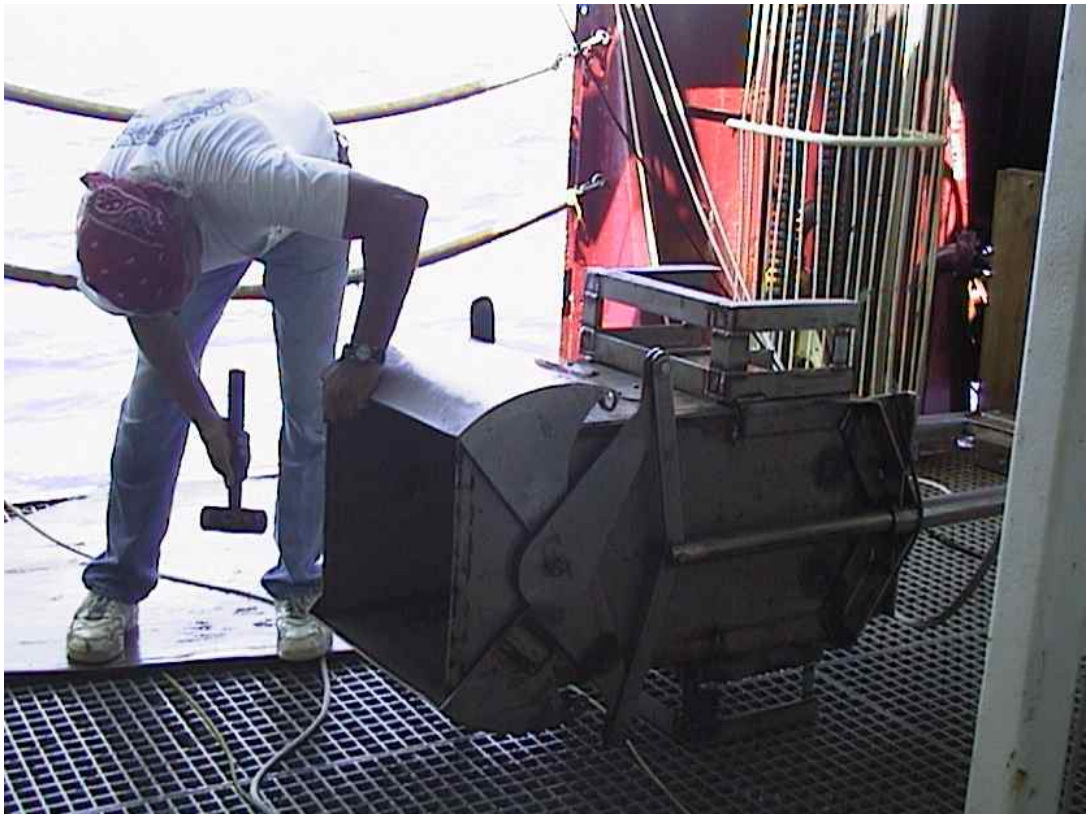

Fig. 4. GOMEX boxcorer. The device is resting on its side, with clamshell doors open.

2.1.3. Benthic Macrofauna

A 0.209 m^2 GOMEX-style boxcorer (Fig. 4) was used to sample benthic macrofauna. At most survey sites, five complete cores were taken. Approximately 0.1725 m^2 from the upper 15 cm of sediment was removed from each boxcore (Fig. 5A), placed in a 30 gallon trash can, and suspended in a filtered seawater/$MgSO_4$ solution. After 20-30 minutes (permitting $MgSO_4$ solution sufficient time to narcotize macrofauna), sample sediments were slowly rinsed through a 300 micron sieve (Fig. 5B). Sieve-retained material was fixed in 10% buffered formalin solution and stored aboard ship for the duration of the cruise.

Upon return to the benthic ecology laboratory at Texas A&M, macrofaunal sediments were freshwater rinsed to remove formalin, and a rose bengal stain applied to mark plant and animal material. Stained sediment was then closely examined under low power stereomicroscope (Figs. 5C, D) by trained macrofaunal sorting personnel. Over a roughly three year period (2000-2003), macrofauna were separated from most DGoMB boxcore samples (Fig. 5E). For each sample core, isolated macrofauna were screened into 43 distinct taxonomic categories (Table 5), labeled, and stored in ethanol.

Precise counts of individual macrofauna were made during the sorting process. This allowed computation of abundance at each survey station for total macrofauna, and taxonomic totals (i.e. total kinorhynchs).

Fig. 5. Processing of DGoMB benthic macrofauna. A. Sediment removed from GOMEX boxcorer. B. Sediments filtered through 300 micron sieve aboard ship. C, D. Retained sediments examined under low power stereoscopes. E. Macrofauna removed from sediment.

Table 5
Types of macrofauna separated from GOMEX boxcore samples.

Amphipoda	Echiura	Ophiuroidea	Zoantharia
Anthozoa	Gastropoda	Ostracoda	Unknown
Aplacophora	Harpacticoidea	Polychaeta	NH-Copepoda*
Ascidiacea	Holothuroidea	Porifera	Pogonophora
Asteroidea	Hydrozoa	Priapulida	Chaetognatha
Bivalvia	Isopoda	Pycnogonida	Halacaridae
Brachiopoda	Kinorhynca	Scaphopoda	Crinoidea
Bryozoa	Mysidacea	Scyphozoa	Hemichordata
Cumacea	Nematoda	Sipunculida	Leptostraca
Decapoda	Nemertini	Tanaidacea	Cladocera
Echinoidea	Oligochaeta	Turbellaria	

* refers to "Non-Harpacticoid" copepods

2.2. Ecologically Important Groups

In order to make more refined ecological assessments of macrofaunal community structure, specific macrofaunal taxa were selected out from the total group and their abundance values separately computed. Eleven taxa were chosen for this, and lumped into three ecological and taxonomic groupings. These are shown in Table 6.

Table 6
Macrofaunal taxa selected for additional analysis.

Polychaete Worms	Sedentary Fauna	Motile Crustaceans
Polychaeta	Bivalvia	Amphipoda
	Porifera	Cumacea
	Scaphopoda	Harpacticoidea
	Scyphozoa	Isopoda
		Ostracoda
		Tanaidacea

2.2.1. Polychaetes

Members of the Class Polychaeta (Figs. 6A1, A2) are usually the dominant macrofaunal group in marine sediments (~50% of total animals, >30% of species), with a rich diversity (Gage and Tyler, 1991). As such, there are obvious choices to select out and measure abundances for separately. Unfortunately, their sheer variety of trophic lifestyles and microhabitat preferences makes them less useful as indicators of specific ecological conditions, unless they are further refined into certain families or genera. The sheer abundance of polychaetes in DGoMB samples made such refinement impractical in the short term. More recent attempts by specialists (specifically F. Hubbard) have resulted in partial workups for each DGoMB survey station. Unfortunately, this work is too incomplete for testing of local diversity patterns.

However, polychaete abundance at the Class level can still be useful. Their densities typically exceed half or more of the entire macrofaunal community within a sediment sample, making them excellent proxies for total macrofaunal abundance (Bhavani et al., 2003; Muniz and Pires-Vanin, 2005). Furthermore, abnormally high or low faunal fractions of polychaetes may indicate ecological competition by other macrofauna (Ingole et al., 2001).

Although members of the Pogonophora (“beard worms”) are now well-argued as members of the Polychaeta, this was not the case when the DGoMB study was designed. As such, pogonophorans were separately identified. Only **76** pogonophorans were isolated from DGoMB sampling, compared with over **65 *thousand*** polychaetes.

2.2.2. Sedentary Fauna (bivalves, poriferans, scaphopods, scyphozoans)

The “sedentary fauna” grouping describes macrofaunal taxa that tend to be less mobile, and (possibly) have a high ratio of suspension and filter feeders. Suspension and filter-feeders can be theorized to prefer deep-sea sediment habitats with higher food content in the near-bottom water column, favoring an epibenthic lifestyle to acquire that food (Gage and Tyler, 1991). They are also likely to favor coarse, less-easily-disturbed sediments (Gray, 1974). The sedentary fauna grouping was used in this study as indicators for more ecologically stable community structure conforming to equilibrium-type processes.

Bivalves. This taxon is also highly abundant in deep-sea sediments. Allen and Sanders (1996) rank it as the second most common macrofaunal group, between polychaetes and peracarid crustaceans. Over **8,000** macrofaunal-sized bivalves were identified from DGoMB boxcores (Figs. 6B1, B2), making them one of the more dominant taxonomic groups. Although specific trophic modes were not determined for individual specimens, it is likely that most were either deposit or filter feeders, and most were capable of limited movement using their muscular foot.

Poriferans. Unlike most macrofauna, sponges (Fig. 6B3) were difficult to quantify as discrete animals. Their general body plan asymmetry and ease of fragmenting likely led to considerable under and over-sampling error, although this cannot be verified. **1,171** “whole” poriferans were identified.

Sponges are filter feeders, and deepwater species are predominantly epipsammic. They are one of the few macrofaunal groups that are incapable of moving on their own.

Scaphopods. "Tusk shells" (Fig. 6B4) tend to prefer dwelling in coarse sands, with either an epibenthic or near-epibenthic (their posterior protrudes out) lifestyle. Coarser sediments help to anchor the shell vertically for near-epibenthic species; the greater interstitial spaces in sandier sediments also facilitate greater use of the feeding captacula. Scaphopods are primarily selective particle feeders. Although not very common in the deep Gulf of Mexico, scaphopods were not particularly rare either. **734** macrofauna-sized tusk shells were identified from boxcores.

Scyphozoans. Sediment-dwelling members of this Class are in the polyp life history stage; polyps can be either feeding or reproductive types. The vast majority of the **14,376** scyphozoan polyps encountered were of the reproductive (strobila) type (Fig. 6B5). While this stage does not feed, it does require a fairly stable, epibenthic location in order to effectively release medusas into the surrounding water column. Strobilas are usually incapable of movement on their own.

Other "Sedentary Fauna". Although other macrofauna taxa (i.e. brachiopods, ascidiaceans, hydrozoans) could have been included in the "sedentary fauna" grouping, most of these tended to be quite rare and were not deemed numerically useful enough to make an impact with hypothesis testing.

Bryozoans were a special case. Although known to be relatively common in deepwater sediments (verified in DGoMB cores), their colonial lifestyle and ease of fragmentation made quantification even more difficult than with poriferans. As such, bryozoans were omitted from refined hypothesis testing.

2.2.3. Motile Crustaceans (amphipods, cumaceans, harpacticoids, isopods, ostracods, tanaidaceans)

"Motile crustaceans" is a created group comprising six taxa that make up the majority of DGoMB macrofaunal crustaceans (and arthropods). Members of these groups tend to be more ambulatory than most other macrofauna, which likely well suits them in exploiting local deadfall or other patchy nutrient sources. Most are detritivores and scavengers. The motile crustacean grouping was used in this study as an indicator for physically and/or biologically disturbed macrofaunal communities conforming to disequilibrium-type processes. Four of the six selected crustacean taxa (amphipods, isopods, tanaids, cumaceans) were peracarids, ranked by Allen and Sanders (1996) as the third most dominant macrofaunal assemblage.

Amphipods. Like their megafauna-sized counterparts (Fig. 6C1), many macrofauna-sized amphipod species are highly active scavengers. If not scavengers, most amphipods are likely to at least be facultative detritivores. Over **34,000** amphipods were counted from DGoMB boxcores. Over half of these were sampled from a single survey station (MT1,

upper Mississippi Canyon). Unfortunately, incomplete datasets precluded this faunistically unusual survey station from diversity hypothesis testing.

Cumaceans. This group was the least abundant "motile crustacean" taxon (**1,311** animals), but also among the largest in size and very distinct in appearance. Cumaceans tend to be either filter feeders or particle feeders; this could argue their inclusion into the "sedentary fauna" group more than that for "motile crustaceans". The author chose to place cumaceans among the latter, reasoning that their increased mobility was more ecologically important than trophic behavior.

Harpacticoids. Among the smaller-sized macrofauna (and often argued as meiofauna), harpacticoid copepods (Fig. 6C2) were one of the most abundant taxa (**15,770** specimens). This group is primarily interstitial, although epibenthic (and even planktonic) forms are known. Unlike other copepod types found in DGoMB cores, anything identified as a harpacticoid was assumed to be benthonic in origin. Like many amphipods, isopods, and tanaids, harpacticoids are predominantly detritivores.

Isopods. **4,179** of these crustaceans were found in boxcores. Isopod body form and feeding habit tend to be highly variable (Figs. 6C3, C4); known trophic modes include scavenging, detritivory, carnivory, and even herbivory.

Many DGoMB specimens identified as isopods were very likely amphipods or tanaidaceans that were damaged and/or missing appendages. By combining these three taxa as part of the “motile crustacean” group, such identification error was eliminated.

Ostracods. “Seed shrimp” (Fig. 6C5) are primarily interstitial and epibenthic, with some swimming forms. Easily distinguished from all macrofauna (excepting bivalves), **6,688** individual specimens were screened from boxcore sediments. Ostracods are scavengers and particle feeders.

Tanaidaceans. “Tanaids” (Fig. 6C6) were one of the more consistently abundant macrofaunal taxa; over **11,000** were identified. They share similar trophic lifestyles to isopods and amphipods, which they closely resemble. Some tanaids are also known to be predators or filter feeders.

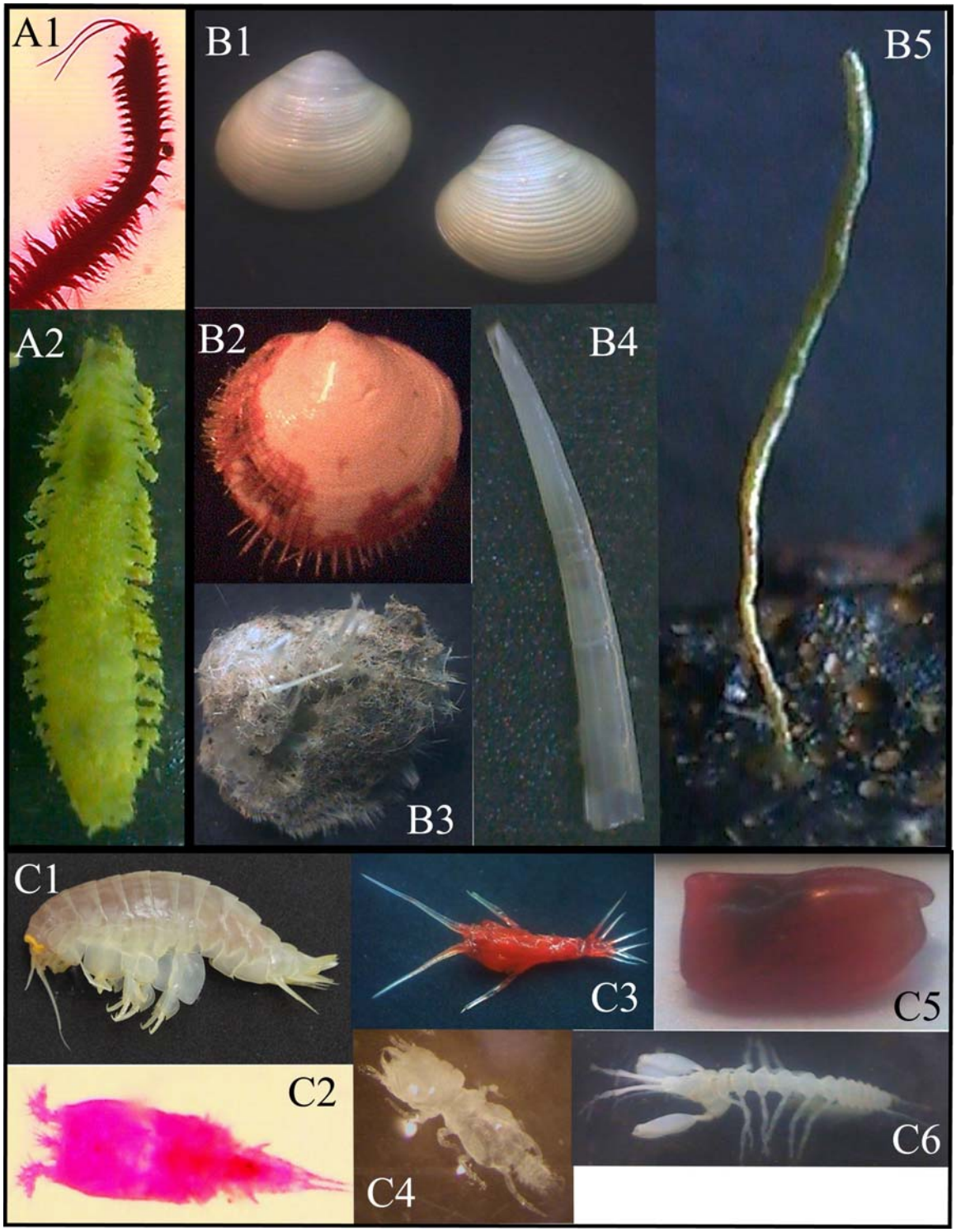

Fig. 6. Taxonomic groups selected for additional macrofaunal analysis. Animals are not shown to scale. Polychaetes: A1, A2. Sedentary Fauna: B1, B2 bivalves; B3 poriferan; B4 scaphopod; B5 scyphozoan strobila. Motile Crustaceans: C1 amphipod; C2 harpacticoid copepod; C3, C4 isopods; C5 ostracod; C6 tanaidacean.

Other "Motile Crustaceans"

Halacarids were probably at least as ambulatory as the "motile crustaceans", but were rarely encountered (**210** found in boxcores). These arachnids were only included in total macrofauna measurements.

Mysids and decapods were even less frequently found than halacarids. Only **22** mysids and **75** decapods were counted. Like halacarids, these taxa were not included among the "motile crustacea" test group. It is likely that most of the mysids were the result of boxcore contamination with the water column.

2.3. Macrofaunal Analyses Performed

Macrofaunal measurements were used from 32 DGoMB survey stations (Table 4). At each of these stations, five complete boxcores were taken, totaling 160 boxcores total. Each of these cores were screened of macrofauna, sorted (by individual boxcore) into the 43 faunal categories listed in Table 5. Over **130,000** individual macrofaunal size-class organisms were identified from these 160 boxcores.

Table 7 lists all of the macrofaunal measurements used for hypothesis testing. These are described further.

Table 7
Macrofaunal measurements used in hypothesis testing.

Total Macrofauna	**Selected Ecological Groups**
Mean Total Abundance	Mean Abundance
Pooled Taxonomic Richness	Coefficient of Abundance Variance
Mean Taxonomic Richness	Abundance Dominance
Taxonomic Within-Site Patchiness	
Mean Taxonomic Diversity	

2.3.1. Mean Abundance (uN)

Mean abundance was calculated for total macrofauna, and for each of the three ecological groupings. Mean abundance refers to the mean macrofaunal abundance value calculated between five separate GOMEX boxcores taken at each survey station (Rowe, in review).

2.3.2. Coefficient of Abundance Variance (Within-Site Abundance C.V.)

Coefficient of abundance variance was calculated for each of the three ecological groupings at each survey station. Also known as "relative standard deviation", c.v. is calculated as follows:

$$C.V. = Standard\ Deviation / Arithmetic\ Mean$$

C.V. was chosen over standard deviation or variance to measure within-site variability, as c.v. is independent of measurement scale used. Thus, abundance variability between DGoMB sites can be directly compared with one another. To simplify intuitive use of this measurement by the author, all c.v. values were expressed as percentages, by slightly modifying the base equation:

$$C.V. = (Standard\ Deviation / Arithmetic\ Mean) \times 100$$

Conversion of c.v. into percentage form is a common practice in statistics (Dytham, 1999). Coefficient of abundance variance was one of two methods used to study local-scale community heterogeneity (or patchiness) of the macrofauna. Unlike turnover diversity (the 2nd patchiness measure), abundance variance does not differentiate

between *types* of macrofauna. This was partially solved by performing separate abundance variance calculations for each of the three ecological groupings.

2.3.3. Taxonomic Richness (mean and pooled)

Taxonomic richness is a derivation of (S), standard species richness (# of species sampled), substituting the macrofaunal taxa identified in the laboratory (Table 5) for discrete species. Both mean and pooled richness values were calculated for each survey station.

Pooled Taxonomic Richness

Pooled taxonomic richness was calculated by summing individual richness values from all five within-site boxcores. This gave a local-scale taxonomic richness value equivalent to 0.8625 m^2 of seafloor, as opposed to the 0.1725 m^2 from a single boxcore.

Mean Taxonomic Richness

Instead of combining the taxonomic richness values at each survey station, the *average* richness value between the five within-site boxcores was taken. Like pooled richness, mean richness values were required to calculate turnover diversity (beta).

Pooling within-site values has the advantage of increasing the sample area, and thus reducing the risk of undersampling. Conversely, taking the mean value from within-site subsamples reduces the penalty incurred from highly divergent within-site subsamples. It also permits the ability to analyze within-site variation. Generally speaking, pooling subsamples is less “risky” with large subsamples that adequately represent the local

ecology. Of course, if the subsample does this, it obviates the need to pool it with other subsamples in the first place.

Pooling subsamples can also be advantageous in fairly homogeneous habitats, where subsample measurements should not be too dissimilar from one another. High similarity between adjacent subsamples would tend to indicate a uniform environment, and pooling adjacent small subsamples together could be reasonably assumed to equate with the taking of one larger sample. The advantage to this is that smaller sampling equipment can be used, and sample area can be scaled down.

2.3.4. Taxonomic Within-Site Patchiness (beta)

Using the sorted macrofaunal taxa as (rough) proxies for discrete species, determinations of *taxonomic* patchiness within each survey site were made. This was done by calculating **beta diversity**, also known as "turnover diversity".

$$\beta = TR_{Spooled}/(TR_{Smean})$$

where $TR_{Spooled}$ is the pooled total number of taxa (or taxonomic *richness*) within a sample site, and TR_{Smean} is the mean number of taxa found between the five within-site boxcores. This is a multi-sample derivation of Whittaker's (1960) original beta diversity equation, thoroughly reviewed by Wilson and Schmida (1984) and Gray (2000). Each replicate series yields one beta measurement, which is directly compared against other sampling stations. Higher beta values indicate less taxonomic commonality between replicate samples, which in turn indicates patchiness (faunal microhabitats within the sampling area).

A potential weakness of *beta* (and other intra-site patchiness calculations) in our study involved precise placement unknowns for the GOMEX boxcores. The GOMEX boxcorer is surface-deployed at an approximate latitude/longitude position, but the deeper the device has to travel in the water column, the greater the tendency for it to swing out of precise position. Water currents and surface sea state also degrade precise core placement. Excluding sea state and water currents, it is likely that replicate corings at deeper sites would have a greater areal dispersion on the seafloor than much shallower ones. However, there was no way to compensate for this potential source of error, other than understanding that it could lead to exaggerated intra-site patchiness calculations as a function of water depth.

2.3.5. Mean Taxonomic Diversity (Taxonomic "Metadiversity"; H')

Measuring diversity is often more useful ecologically, as diversity takes into account not only the number of species (or in this case, taxa) in a sample, but also the proportional distribution of the *individuals* among the taxa (Gray, 2000). The Shannon-Weiner information function is one of the more widely used diversity measurements, and is relatively scale-independent.

$$H' = -\Sigma((n_i/N) \times (\log(n_i/N)) \qquad (n_i = \text{number of individuals per taxon})$$

$$(N = \text{total number of } \underline{\text{all}} \text{ individuals})$$

Although not considered as statistically robust as species-level calculations (higher-level taxonomy being somewhat more subjective than genus/species-level taxonomy), use of

higher-level taxa is common within the macrofaunal survey literature (Hessler and Jumars, 1974; Grassle and Maciolek, 1992; Kukert and Smith, 1992; Borowski and Thiel, 1998, Doerries and Van Dover, 2003; Narayanaswamy et al., 2003). It is usually much easier to isolate and identify higher-order taxonomic groups from large sediment samples than it is to identify at the genus or species-scale.

For purposes of this study, the taxonomic diversity measurement was referred to as "taxonomic metadiversity" (shortened to "metadiversity"). Metadiversity is a bioinformatics term used to denote the organization of different types of data pertaining to biological diversity (Kaser & Cox, 1999). As this study's measure of diversity relied on such a wide-ranging spectrum of invertebrate taxa (> 40) and taxonomic *levels* (> 3), use of this meta-data term was viewed by the author as applicable.

2.3.6. Abundance Dominance (% Dominance)

For each of the three ecological groupings of macrofauna, an abundance dominance value was calculated for each survey station. This was simply the ratio of mean abundance of each ecological group (i.e. polychaetes) to total mean macrofaunal abundance, converted into a percentage.

$$\%\ Dominance = (uN\ (ecological\ grouping) / uN\ (total\ macrofauna) \times 100$$

Abundance dominance is a highly effective tool for examining community structure patterns and changes (if any) between the three test ecological groupings of polychaetes, sedentary fauna, and motile crustaceans.

2.4. Statistical Testing and Mapping

2.4.1. Statistical Testing

Choice of statistical design and examination procedures were taken from Dytham (1999). Non-parametric correlation analyses (Kendall's *tau*-b) were performed to identify associations between test variables. Kendall's *tau* is similar to the more popularly used Spearman's rank-order correlation, but has the advantage of performing partial correlations.

Correlations greater than 0.20 were selected for regression testing. This minimum value was selected after preliminary regressional testing showed that correlations less than 0.20 did not yield linear regressions supported by ANOVA analysis (F-value less than 0.05). Regression testing with single, causal (independent) variables was performed to seek out statistically significant relationships to support/refute hypothesis testing. With few exceptions, Model I linear regression models were adopted as a standard, with the r^2 measures used as strength of relationship indicators. For this study, regressional r^2 values less than 0.14 were deemed "not significant", and not plotted. This value cutoff was selected after observing that regressional test variables possessing r^2 values less than 0.14-0.15 almost always were not supported by ANOVA analysis (F-value greater than 0.05). Regressional r^2 values at or exceeding 0.20 were judged by the author as sufficient for general use in tables, as this minimum value was always supported by ANOVA analysis. The advantages of adopting one regressional model (linear) were that test results between multiple dependent variables could be shown together within a single

table. This was deemed highly useful, given the large number of test variables. Preliminary examinations with other regression types (i.e. Model II polynomial, logarithmic) were done, but proved to be less useful except in a few cases.

Linear regression assumes independent (cause) and dependent (effect) relationships between compared test variables (Dytham, 1999). In some cases during this study (i.e. bioturbation and macrofaunal abundance, abundance dominance and taxonomic diversity), it was unclear which variables were best argued as being independent vs. being dependent of one another. This was particularly true when comparing macrofaunal community measurements against one another. Laws and Archie (1981) discuss the problems of using uncontrolled independent variables in regressional analysis. In particular, they show that in cases where correlation coefficients are low, Model I regressional slopes tend to be underreported.

However, the author's study was primarily exploratory and less concerned with predicting the *rate* of change (or the slope) between test variables than it was with seeking the *strength* of potential relationships (determined by r^2) and general trend between those variables. For the former (r^2), this is simply the coefficient of determination between X and Y variables, and is calculated the same way for Model I and Model II linear models. In the case of looking at trends in the slope of the linear model, potential differences between Model I and Model II regressions were considered by the author as less important than the overall trend pattern itself.

Regarding instances where determination of the dependent and independent variables was problematic, this was of little actual concern, as linear r^2 values are unaffected by reversing variables on X-Y plots.

The Kolomogorov-Smirnov (K-S) test was used to verify assumptions of normally distributed test variables. Some test variables (i.e. POC) were LOG_{10}-transformed to improve normality distributions for regression testing. SPSS (vers.11 & 14) and Microsoft Excel 2002 Data Analysis Pack were the statistical packages used. Scatterplots were produced using Microsoft Excel 2002.

2.4.2. Mapping

Gulf-wide maps showing DGoMB survey sites were produced using ESRI ArcMap 8.1. Single-site test measurements (i.e. abundance) were graphically illustrated with graduated symbols, classified using the default “natural breaks” setting. Comparisons between different physiographic regions (i.e. canyons vs. non-canyons, eastern GoM vs. western GoM) were only crudely examined via visual examination (by the author) of these maps. This was primarily due to indecision on the author’s part on how to accurately delineate discrete “cutoffs” between survey stations within physiographic regions.

This was an important concern, for several reasons. The effects of water depth (which often varied enormously between sample stations) had the potential to mask out regional patterns or create bias towards sample regions with uneven depth profile regimes. Roughly half of the eastern GoM stations were located within submarine canyons, which

could easily bias latitudinal comparisons. Regarding submarine canyons themselves, each of the three varied greatly in size from one another, two were inactive relict systems, and one canyon was only represented by a single DGoMB site at a lower slope depth. DGoMB survey sites were clumped in a manner making it difficult to separate "eastern" vs. "western" GoM. For instance out of the 32 sites the author examined (Fig.1, Table 4), one-third of these (11) were more "central" GoM. Half of these (the "C-series") could be (and have been by other researchers) argued as being "eastern GoM" and the other half "western GoM", or one/both sets removed from an eastern vs. western comparison entirely.

Preliminary ANOVA analysis by the author of physiographic regions using different delineating criteria often yielded opposing results. These early tests were viewed by the author as excessively confounded by a combination of very distinctive individual survey sites, water depth effects, and unevenness of physiographic regions. As such, the author viewed statistical comparisons of DGoMB-specified regions as unreliable and did not perform them.

The DGoMB final program report (Rowe, in review) did make discrete physiographic delineations in its initial test design and carried out statistical examination of them, but more recent analyses using cluster techniques are indicating that many of these are inappropriate or imprecise. As these program results are not yet finalized, the author chose to take a cautious approach with physiographic comparisons and minimize fixed zone delineations as much as possible. Although relegating physiographic comparisons

to simple visual analysis prevented the author from statistically isolating weaker regional patterns, it allowed much greater interpretative flexibility of them.

2.4.3. Photographic Analysis

Seafloor photographs taken with the Benthos DSC 4000 camera were used to crudely evaluate benthic bioturbation (biologically-derived sediment mixing) at each DGoMB study site. Over 1,000 digital photographs were visually ranked within five surface bioturbation categories (Fig. 7). Presence, quantity, and size of specific lebensspuren (mounds, burrows) were the most important criteria for ranking bioturbation. Mounds and burrows were specifically focused upon due to their implied high sediment mixing, ease of identification, and evidence from other studies that they (mounds) were known to have an effect upon infaunal community structure. Smith, Jumars and DeMaster (1986) and Kukert and Smith (1992) experimented extensively with natural and artificial mounds in the Santa Catalina Basin in the eastern Pacific, and reported considerable sediment re-working and enhanced macrofaunal diversity associated with them.

Rather than attempt to directly quantify bioturbation by precisely counting mounds and burrows as was done for NGOMCSS (Galloway, Martin and Howard, 1988), or by total percent cover of lebensspuren (Ziegler, 2002) it was decided that a more qualitative approach using key identifiers (Fig. 7) would be more effective. This method reconciled potential problems with frame size variation and incomplete images in the DGoMB camera system, and also placed greater emphasis on burrow and mound *size* rather than just simply enumerating the numbers of burrows and mounds. As burrow/mound

features could vary in size by almost an order of magnitude, it was viewed by the author that larger bioturbation features should necessarily be linked with a higher “disturbance weight” than similar feature types of smaller sizes. Preliminary examination of DGoMB photographs also led to the incorporation of more anecdotal qualifiers (sediment color, stippling) into photographic ranking criteria. These were selected more for the reason that they tended to loosely match up with sediments showing certain burrowing activity intensities, and were used more as secondary indicators. The photographic analysis method used for this study was specifically tailored for use with DGoMB images, and is not intended for direct application with other seafloor mapping studies.

To test the author’s bioturbation evaluation technique, values from Ziegler (2002) were directly compared. Ziegler used the same DGoMB seafloor images to evaluate bioturbation, but his analysis criteria were different and contained only three rank categories. This is further examined in section 3.8.

Along with photographs taken along the continental slope, images from four abyssal plain sites were examined. These abyssal site photographs were only used for bioturbation measurements, as their physical, chemical and biological measurements followed a different format than that used for the continental slope study and were not compatible for the author’s purposes.

Bioturbation values were used in hypothesis testing as a direct measurement for small-scale habitat heterogeneity, and an indirect measurement for benthic disturbance.

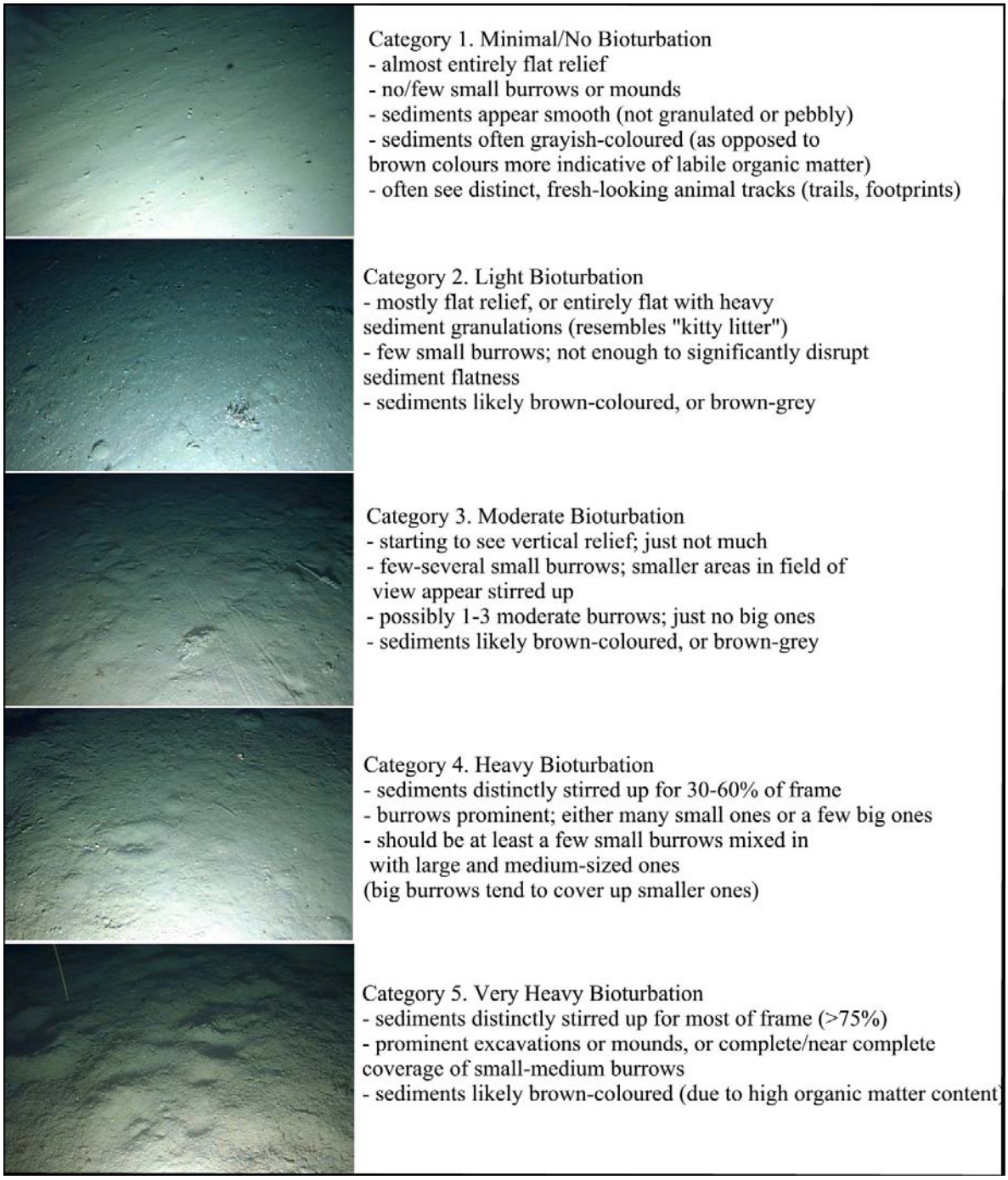

Fig. 7. Test criteria for ranking bioturbation intensity at DGoMB survey stations.

3. RESULTS

3.1. Mean Total Macrofauna Abundance

Station MT3 (mid-slope Mississippi Canyon) reported the highest total mean macrofaunal abundance, at 2,418 organisms (14,017 m^2). The lowest value was at the bottom of the same canyon (MT6), with an average of 253 organisms per boxcore sample. Between all 32 survey stations, there was an average of 823 organisms per boxcore, or 5,107 per square meter.

It should be noted that station MT1 (480 m, upper Mississippi Canyon) actually contained the highest measured mean macrofaunal abundance (22,343 m^2). This is 63% higher than the mean abundance found at the mid-slope MT3 site. Unfortunately, the upper-canyon MT1 (and MT2) stations were not analyzed further in this study, due to incomplete data measurements. Only three valid macrofaunal boxcores were taken from station MT1, for example.

Figure 8 shows a negative linear relationship of abundance to water depth. The relationship is stronger when abundance data is LOG_{10}- transformed (Fig. 9).

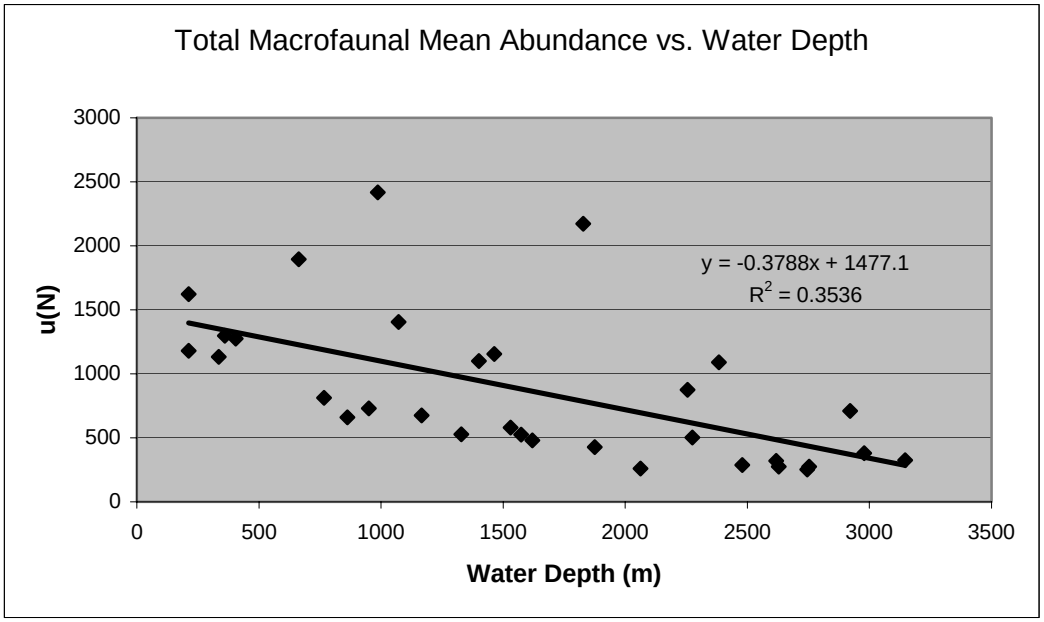

Fig. 8. Total mean macrofaunal abundance in relation to water depth. Abundance values are actual (.1725 m^2).

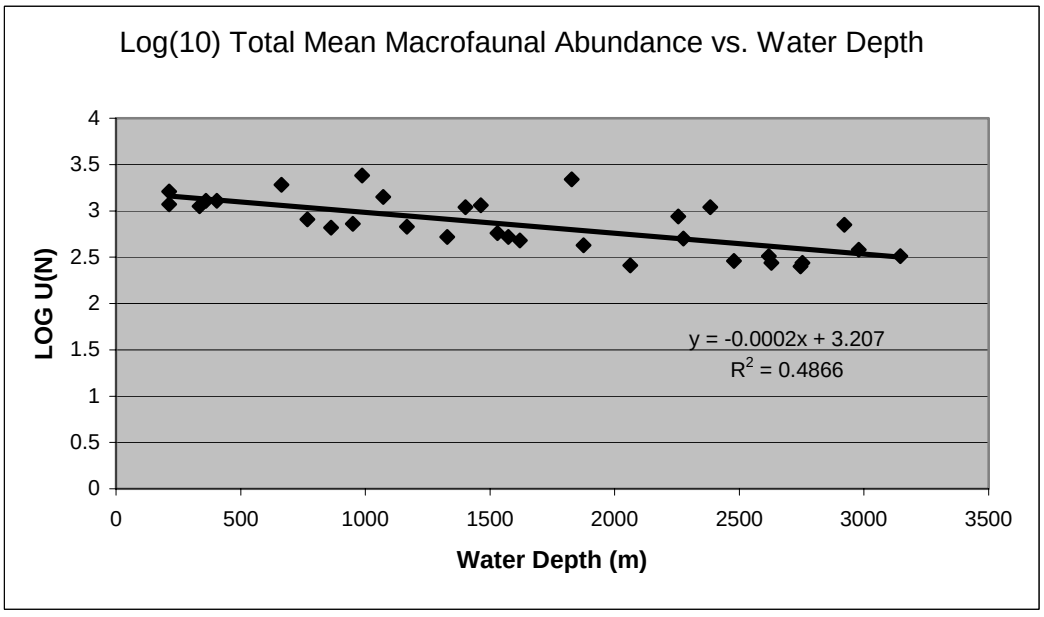

Fig. 9. Total mean macrofaunal abundance (LOG_{10}) in relation to water depth.

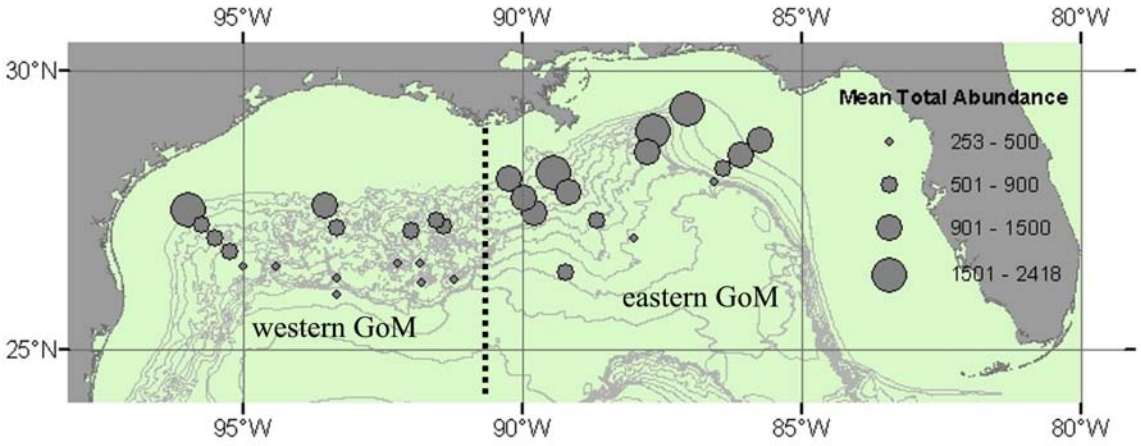

Fig. 10. Mean total abundance patterns for macrofauna. Numbers are for actual sample area (.1725 m^2). Macrofaunal abundance values are generally higher in the eastern GoM.

Northern GoM macrofaunal abundance patterns are illustrated in Fig. 10. Overall, abundance is highest on the upper continental slopes, and lowest on the lower continental slope. The eastern GoM possesses higher abundance than the western GoM. Both the DeSoto and upper Mississippi Submarine Canyons displayed high abundance.

All total mean abundance values were LOG_{10} –transformed for further statistical testing, after normality testing (K-S) showed that LOG_{10}-transformed variables generated more evenly distributed values. Significant regressional relationships to total mean abundance (LOG_{10}) were found in Table 8.

Table 8
Significant (>0.20) linear regressional relationships to total macrofaunal abundance (LOG_{10}).

Test Variable	linear r^2
Water Depth	-0.49
Taxonomic Patchiness (*beta*)	-0.27
Bioturbation	-0.32
POC	0.40 (0.47*)
Mean Polychaete Abundance	0.91*
Mean Sedentary Abundance	0.52*
Mean Motile Crustacean Abundance	0.71*
Motile Crustacean Within-Site Abundance Patchiness (c.v.)	-0.28

* Both variables LOG_{10} transformed

3.1.1. Total Mean Macrofaunal Abundance: Other Relationships

Table 8 shows significant regressional values of test variables with total mean macrofaunal abundance. Other than water depth, negative relationships were also observed for patchiness of taxa (*beta*-scale metadiversity, Fig. 11), and motile crustacean abundance patchiness (Fig. 12).

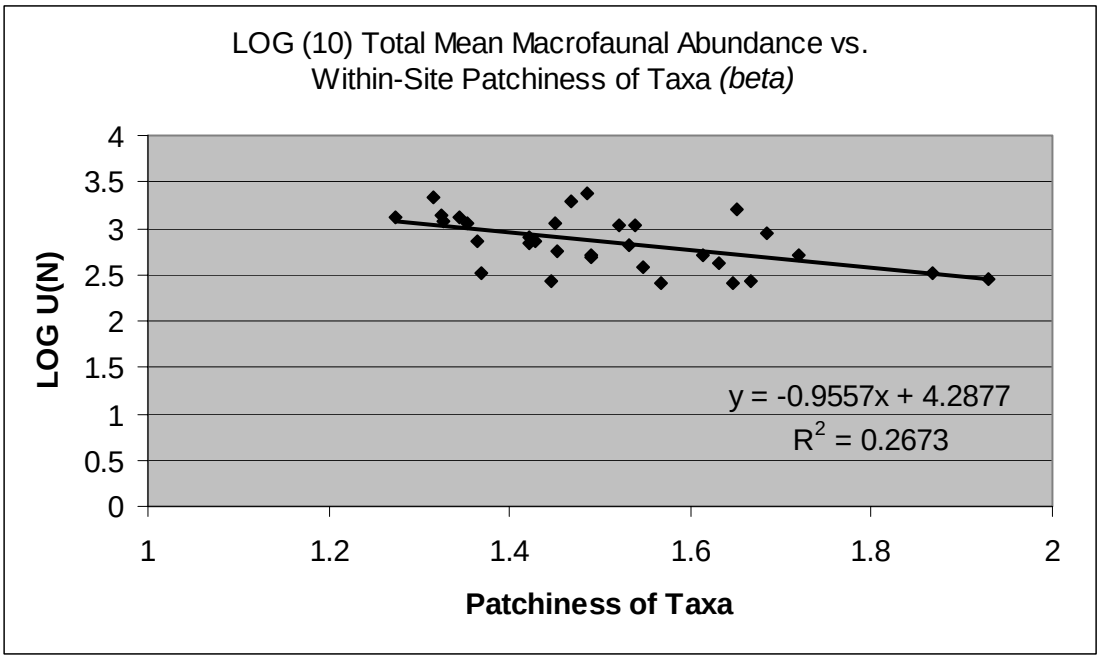

Fig. 11. Total mean macrofaunal abundance (LOG_{10}) in relation to local intra-site taxonomic patchiness.

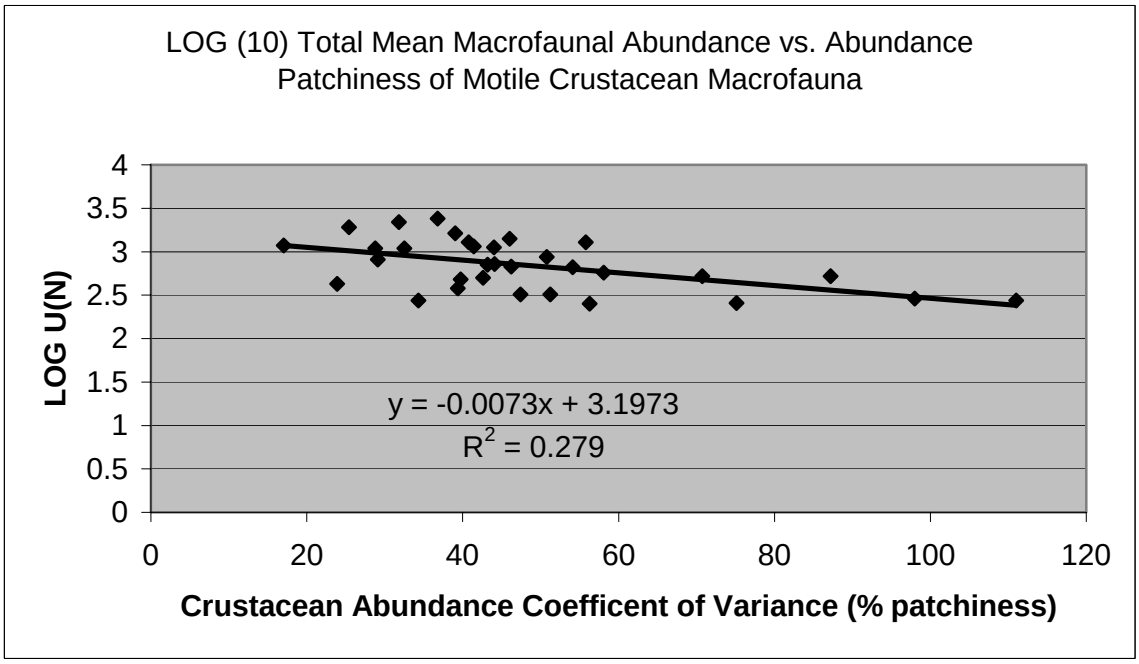

Fig. 12. Total mean macrofaunal abundance (LOG_{10}) in relation to local abundance patchiness of motile crustaceans.

Positive relationships were calculated for bioturbation intensity (Fig. 13) and particulate organic carbon (Figs. 14, 15).

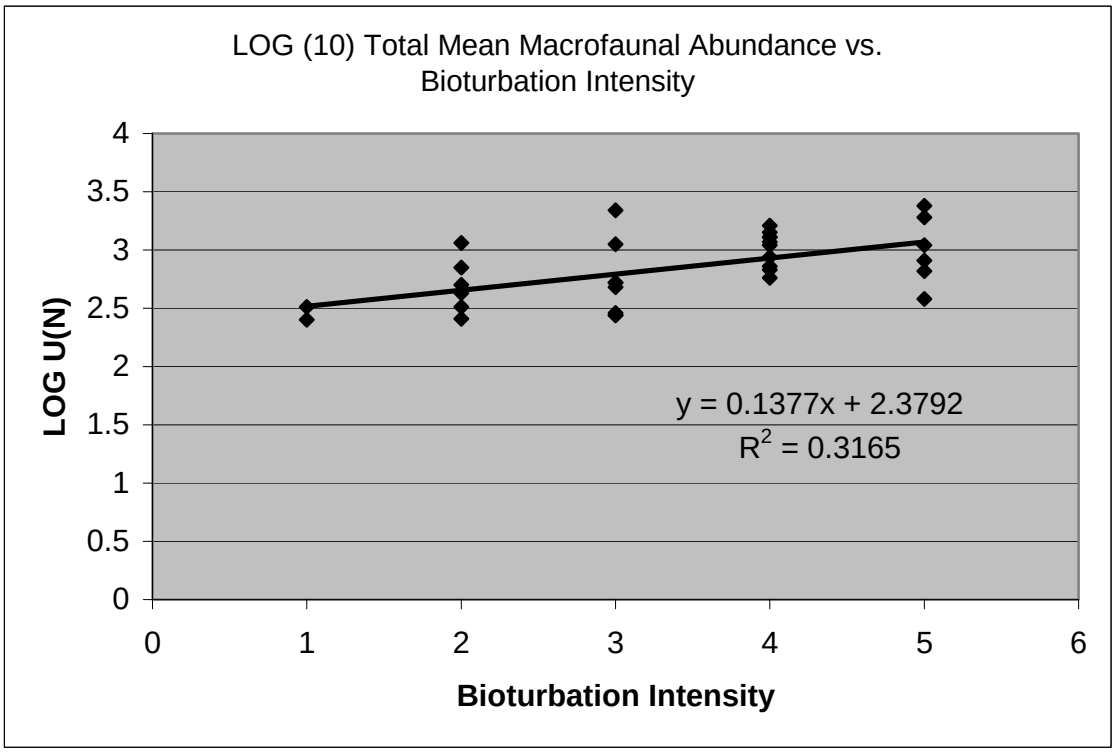

Fig. 13. Total mean macrofaunal abundance (LOG_{10}) in relation to bioturbation intensity.

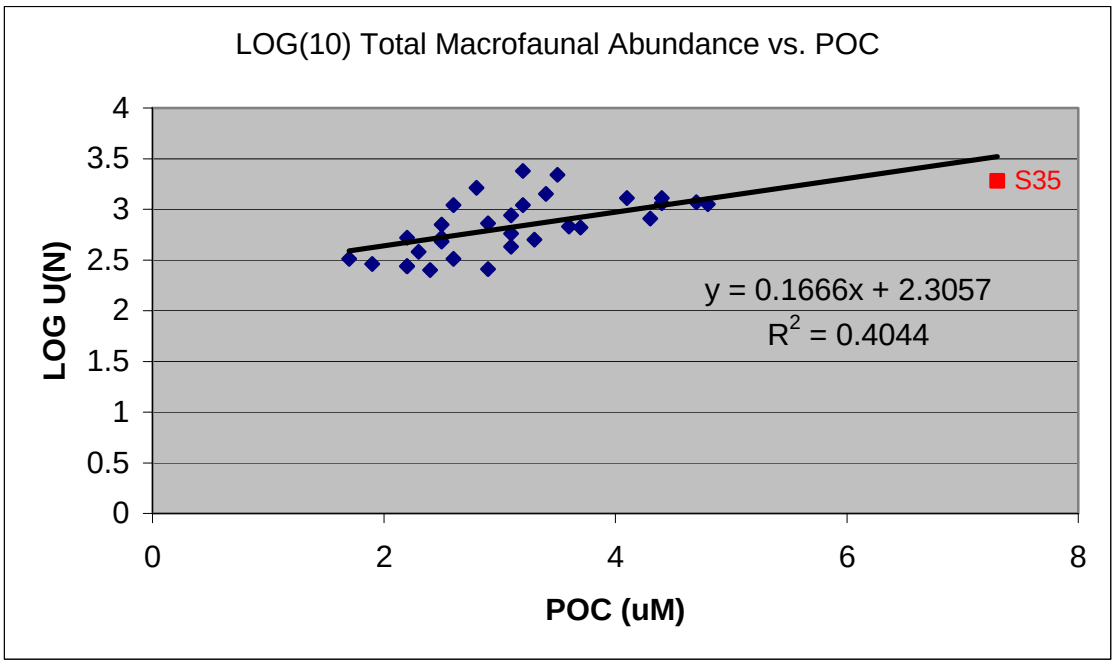

Fig. 14. Total mean macrofaunal abundance (LOG_{10}) in relation to bottom-water POC. High POC value at station S35 (upper DeSoto Canyon) is colored red.

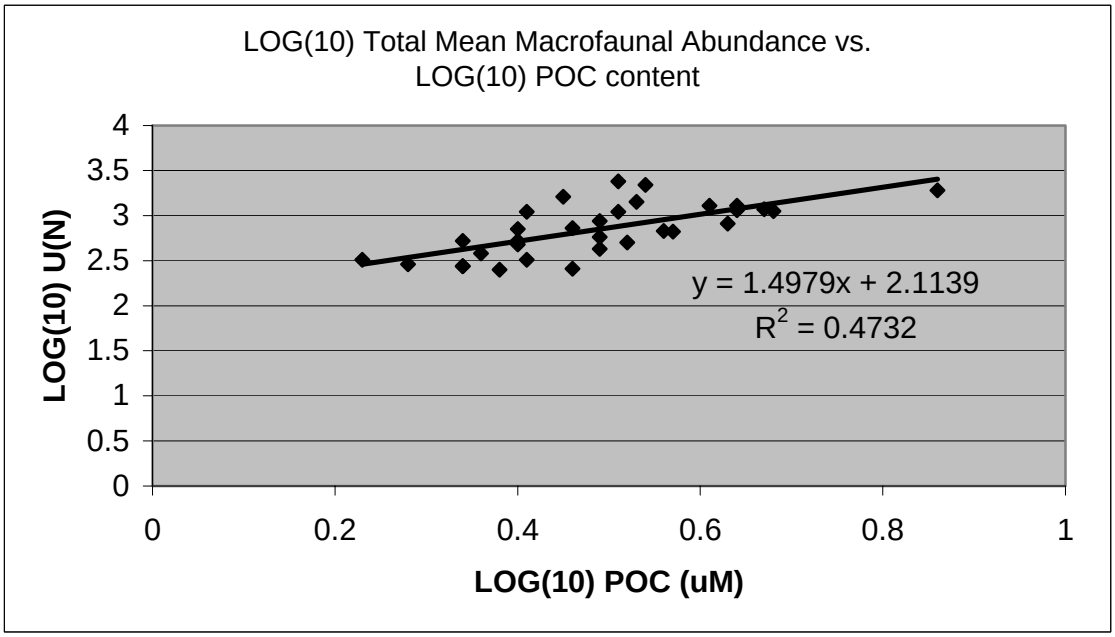

Fig. 15. Total mean macrofaunal abundance (LOG_{10}) in relation to bottom-water POC (LOG_{10}) content.

Mean abundances for polychaete worms (Fig. 16), sessile taxa (Fig. 17), and motile crustacean taxa (Fig. 18) also were positively linked to total mean density, as they generally should be, being directly taken from the same datasets as those used for total macrofaunal abundance.

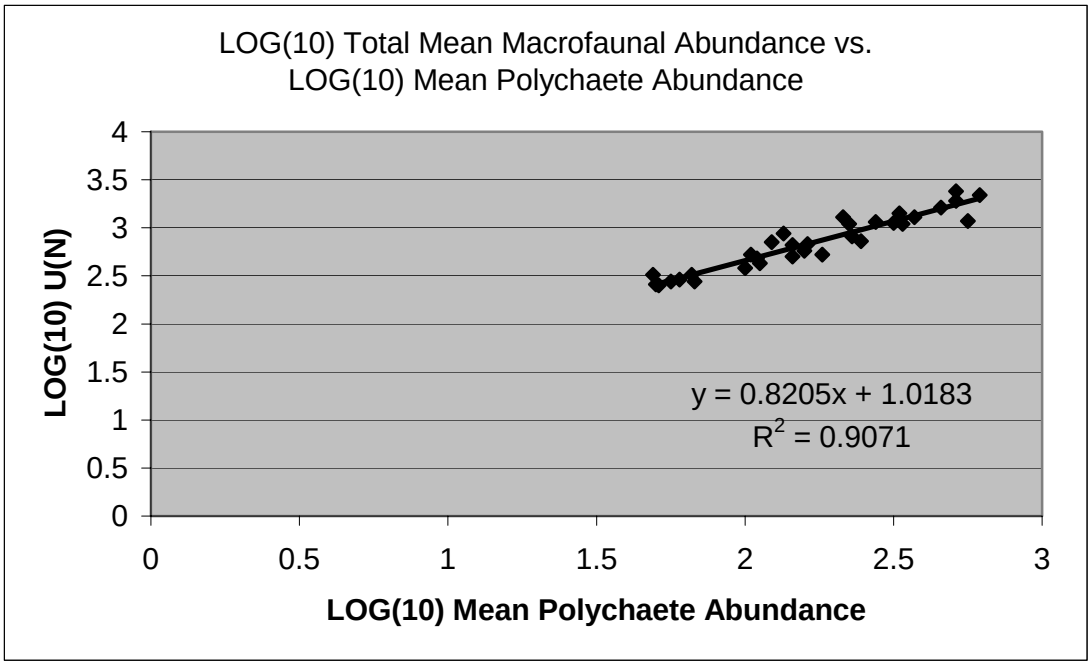

Fig. 16. Total mean macrofaunal abundance (LOG_{10}) in relation to mean polychaete abundance (LOG_{10}). The very strong relationship is likely linked to the high ratio of polychaetes that comprise the total macrofauna.

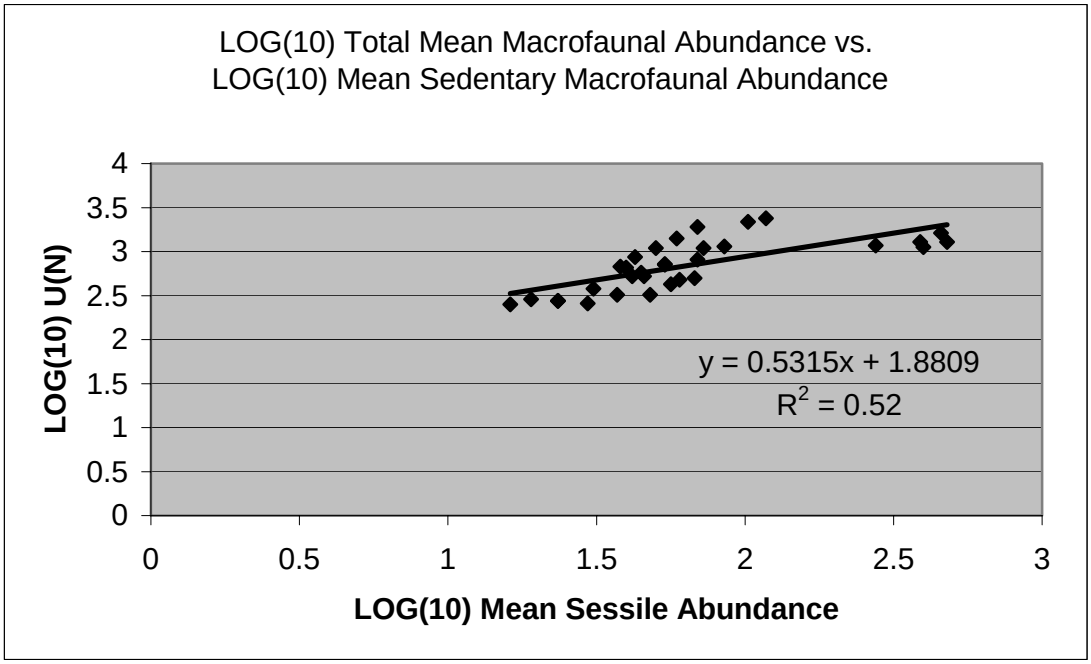

Fig. 17. Total mean macrofaunal abundance (LOG_{10}) in relation to mean sedentary abundance (LOG_{10}).

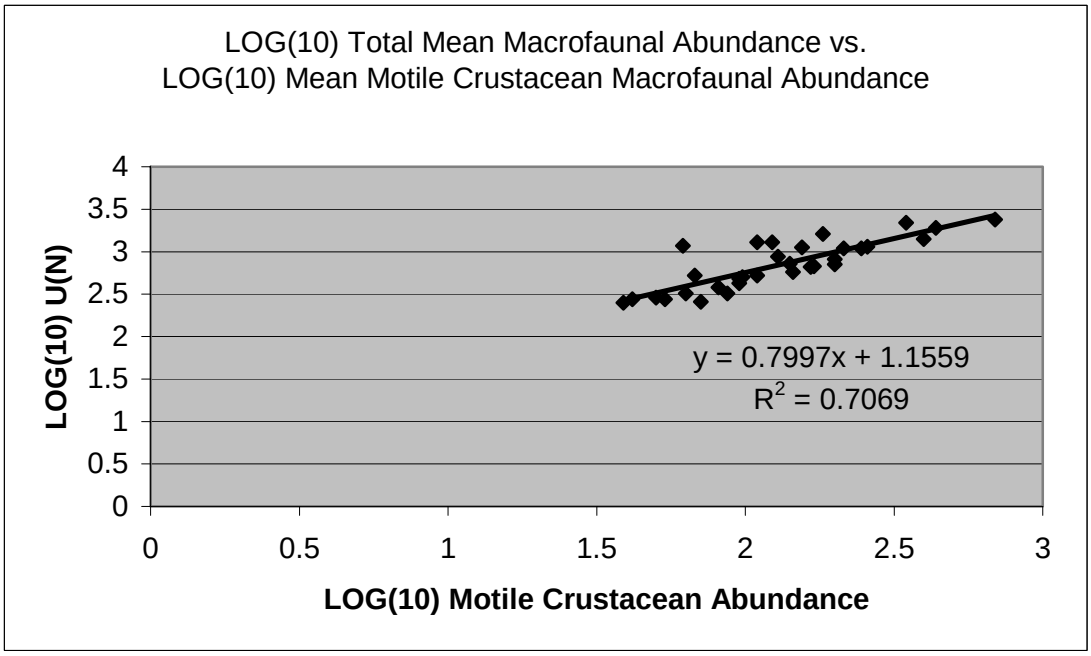

Fig. 18. Total mean macrofaunal abundance (LOG_{10}) in relation to mean motile crustacean macrofaunal abundance (LOG_{10}).

There was no significant correlation of macrofaunal abundance to taxonomic metadiversity, or bottom sediment type.

3.2. Mean Abundance Patterns for Ecologically Important Taxa

Eleven macrofaunal taxa were isolated and lumped into three ecological categories (Table 6). For statistical purposes (improve normality fits), abundance values from all three categories were LOG_{10}-transformed.

3.2.1. Mean Polychaete Abundance Patterns

The most abundant macrofaunal taxon encountered in nearly all samples belonged to the Class Polychaeta. On average, 26% of identified macrofauna taxa comprised polychaete worms. Fig. 19 shows polychaete percent dominance for the northern GoM. The lowest fractions (15-20%) were most common below 2,000 m, although site S43 on the upper Florida Escarpment (361 m) possessed only 17% polychaete dominance. Conversely, adjacent site S44 (213 m) possessed the highest dominance, at 48%. High polychaete dominance (>25%) tended to occur along upper slope depths.

There was no statistically significant relationship to polychaete dominance vs. sediment type. However, the site with by far the greatest polychaete dominance (S44) also contained the second highest sediment sand fraction surveyed (57%). The area possessing the highest sand fraction (MT5) was near the bottom of the Mississippi Canyon, and had 29% polychaete dominance.

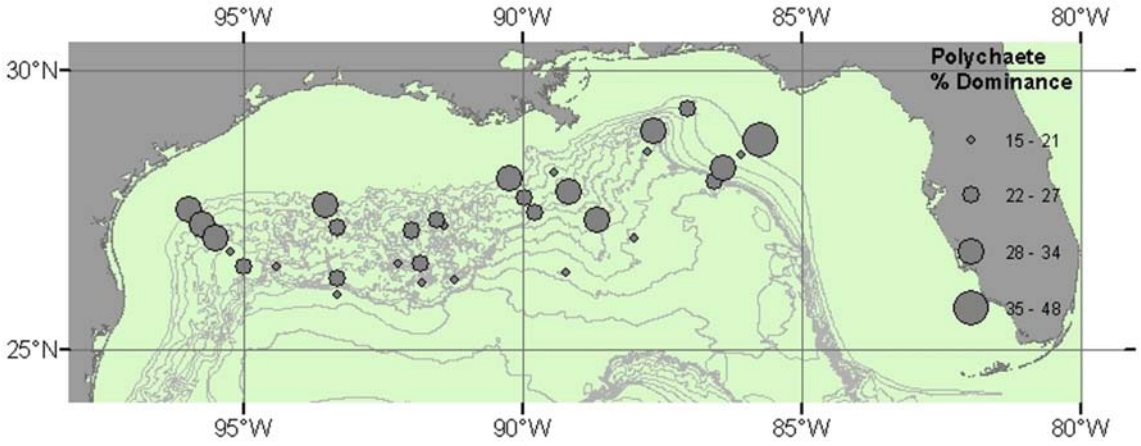

Fig. 19. Macrofaunal percent dominance of polychaete worms.

Mean polychaete abundance varied greatly, from a low of 49 (284 m^2) at basin site B3, to a high of 620 (3,594 m^2) at site S36 in the DeSoto Submarine Canyon. Patterns of polychaete abundance closely mirrored those for total macrofaunal abundance (Fig. 16). Basin-wide polychaete abundance patterns are shown in Fig. 20. Overall, they loosely reflect the patterns seen for total macrofaunal abundance, and polychaete dominance. Higher values are found in upper slope depths, with lowest values in the deepest slope regions (Fig. 21). The DeSoto canyon contained higher polychaete abundance at deeper depths than similar stations in the Mississippi and Alaminos canyons.

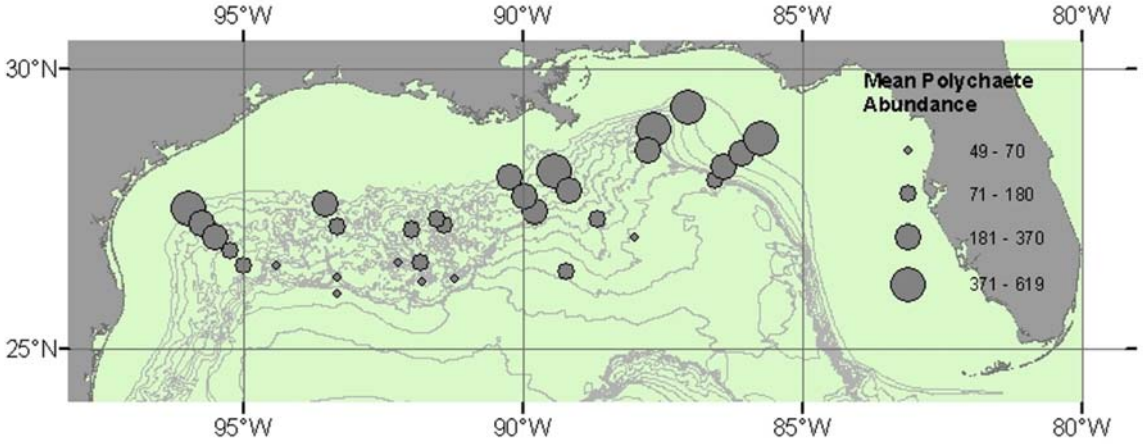

Fig. 20. Mean polychaete abundance patterns. Numbers are for actual sample area (.1725 m^2).

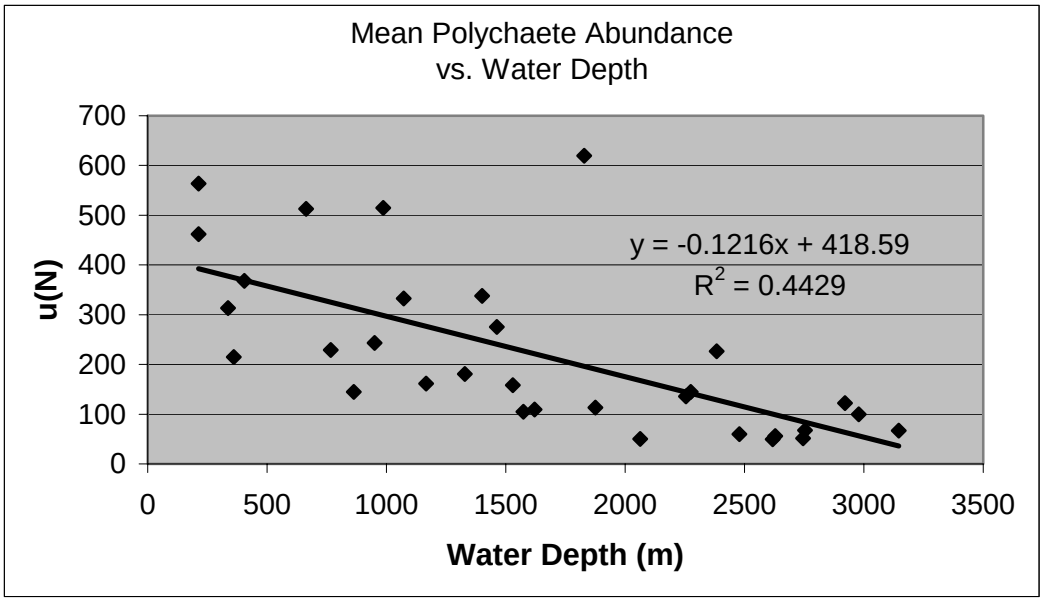

Fig. 21. Mean polychaete abundance in relation to water depth. Polychaete values are actual (.1725m^2).

Significant (linear r^2 greater than 0.20) regressional relationships for polychaete abundance are shown in Table 9. Both within-site patchiness of taxa (beta) and taxonomic metadiversity displayed weak negative (r^2 less than 0.30) regressional

relationships to polychaete abundance. There was a slightly stronger (r^2 =0.36) relation of abundance to burrowing intensity. POC was highly significant (Fig. 22). Abundance of co-occurring motile crustacean macrofauna loosely paralleled polychaete abundance (Fig. 23). There was also a positive relation of polychaete abundance to patchiness of motile crustaceans. Higher polychaete abundances were markedly higher when motile crustacean patchiness was less than 45% (Fig. 24). Polychaete abundance did not correlate with sediment type.

Table 9
Significant (>0.20) linear regressional relationships to mean polychaete abundance (LOG_{10}).

Test Variable	linear r^2
Total Mean Abundance	0.91*
Water Depth	-0.57
Taxonomic Patchiness (*beta*)	-0.24
Bioturbation	0.25
POC	0.47*
Mean Motile Crustacean Abundance	0.54*
Motile Crustacean Within-Site Abundance Patchiness (c.v.)	0.27

* Both variables LOG_{10} transformed

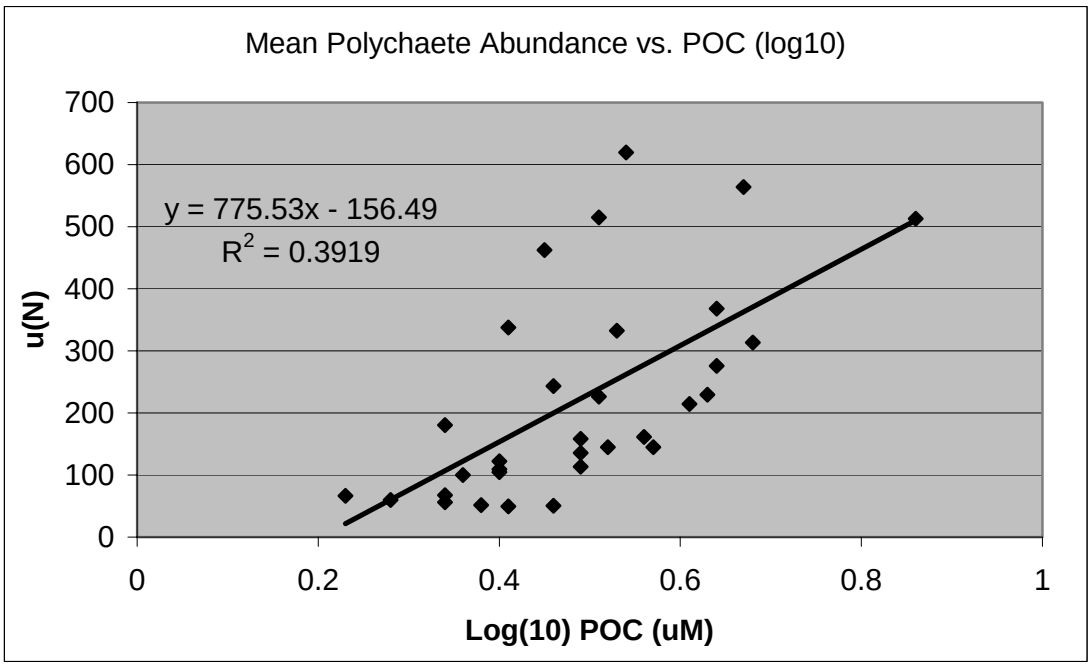

Fig. 22. Mean polychaete abundance in relation to bottom-water POC (LOG_{10}). Polychaete values are actual (.1725 m^2).

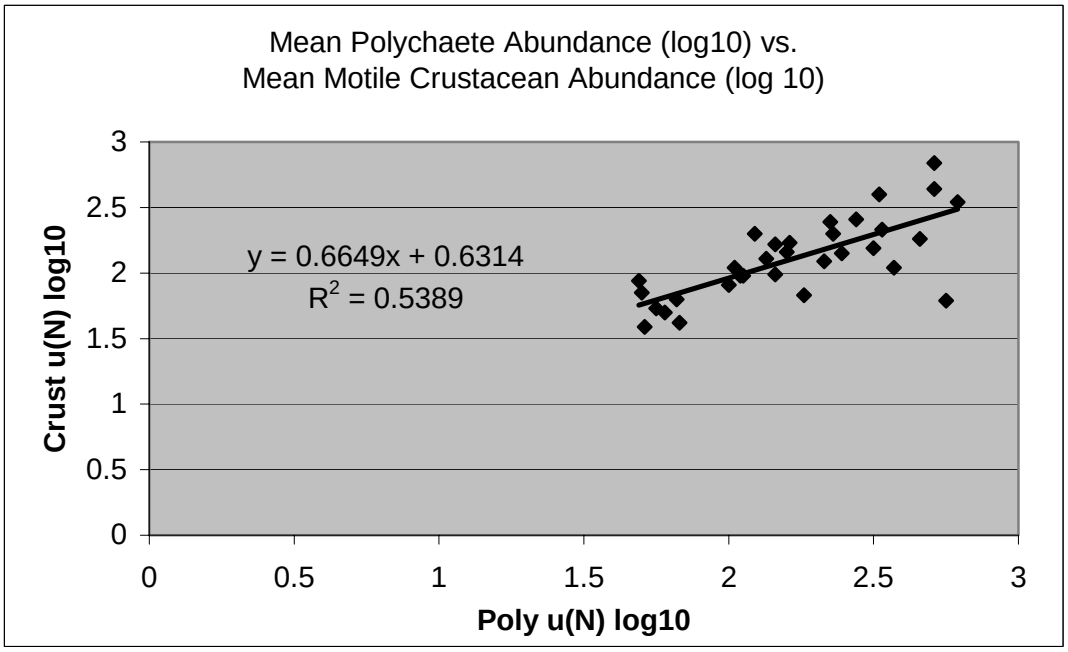

Fig. 23. Mean polychaete abundance (LOG_{10}) in relation to mean motile crustacean abundance (LOG_{10}).

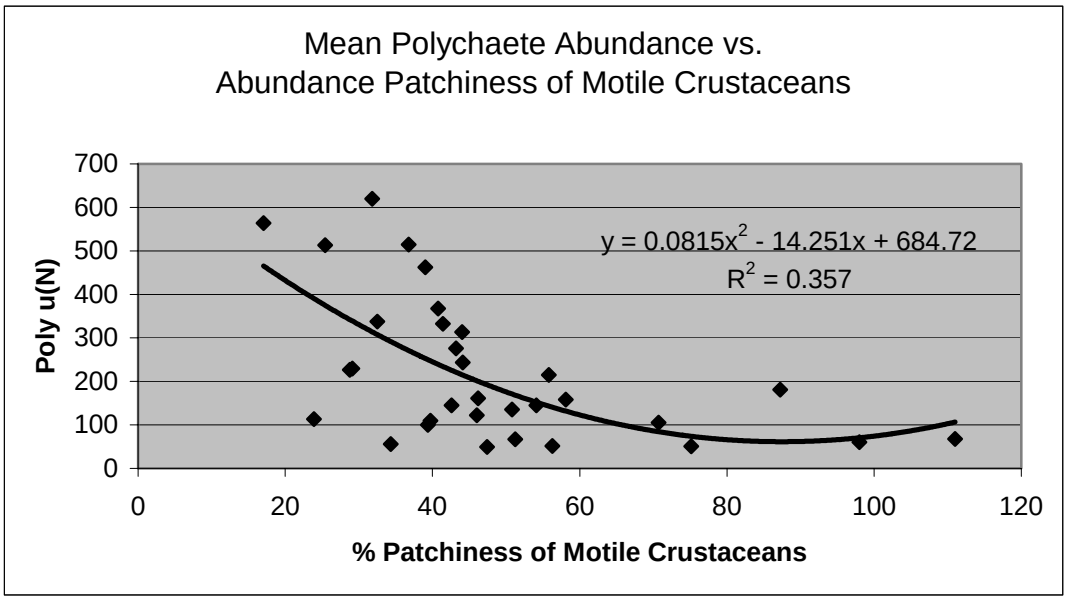

Fig. 24. Mean polychaete abundance in relation to within-site abundance patchiness (c.v.) of motile crustaceans. Polychaete values are actual (.1725 m^2). Regression line used is 2^{nd} order polynomial. Note majority of survey stations possess crustacean patchiness between 40-60%, and high polychaete abundance values only occur at crustacean patchiness values less than 45%.

3.2.1.1. Local-scale Polychaete Abundance Patchiness

Within-site abundance patchiness for polychaetes was measured using its coefficient of variance (c.v.), reported as a percentage (Fig. 25).

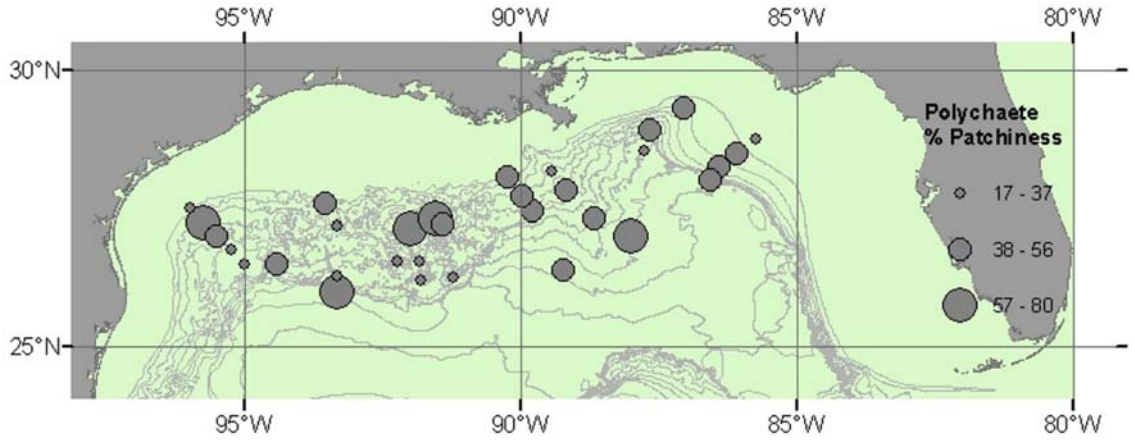

Fig. 25. Within-site patchiness of polychaete abundance. Values are computed as coefficients of variance (c.v.), which are expressed as percentages.

Polychaete abundance patchiness was not statistically correlated with any test factors, nor were any gulf-wide patterns discerned. The majority of sample sites did however possess moderate to high patchiness values (>35%). The mean abundance patchiness value for polychaetes was 45%.

3.2.2. Mean Sedentary Fauna Abundance Patterns

"Sedentary fauna" describes a group of four macrofaunal taxa (Table 6) that share highly limited mobility (relative to other macrofaunal groups). Members of these taxa are predominantly filter or deposit feeders. These organisms are described in Methods.

The sedentary taxa grouping made up a significant fraction of sampled macrofauna at most survey stations. On average, 13% of identifiable macrofauna belonged within this group. Fig. 26 shows sedentary fauna percent dominance for the northern GoM.

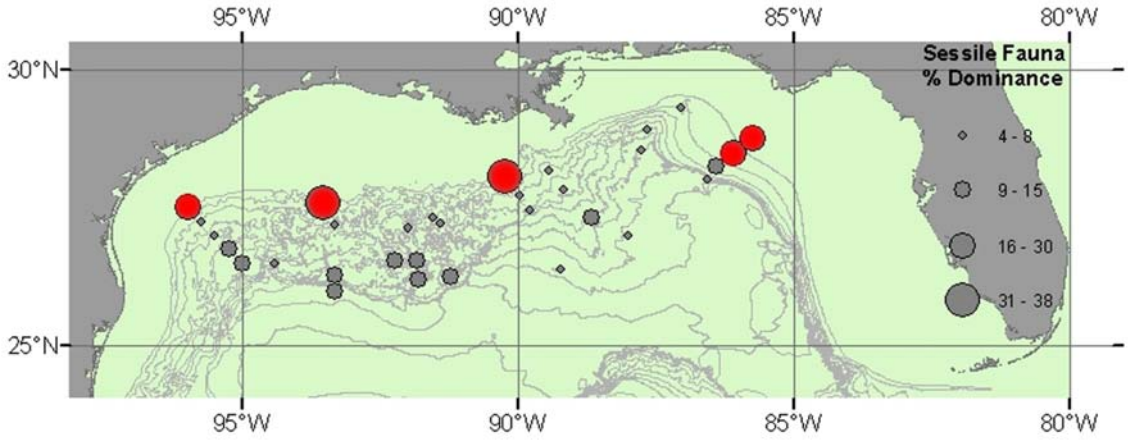

Fig. 26. Macrofaunal percent dominance of sedentary fauna throughout the DGoMB sampling area. The shallowest slope stations (indicated in red) have the highest percentages of sedentary organisms.

The lowest fractions (4-8%) of sedentary fauna were most commonly seen in the northeast GoM, and in submarine canyons. The highest value (13%) within any of the submarine canyon sites was at station MT5 within the lower Mississippi Canyon; all other canyon stations sampled less than 10% of sedentary macrofauna. The lowest percent dominance values overall for sedentary fauna were seen at station S35 in the upper DeSoto Canyon, and at station C7 in the north-central GoM at 1,100 m depth. Both of these sites sampled only 4% sedentary fauna.

High sedentary dominance (16-38%) tended to only occur in shallow sites less than 500 m deep (Fig. 27). Intermediate values (9-15%) were common throughout the mid-lower slope depths in the northwest GoM. The two stations with the highest dominance of sedentary macrofauna (>30%) were W1 (west-central GoM), and C1 (central GoM). Both of these sites are very shallow (<500 m).

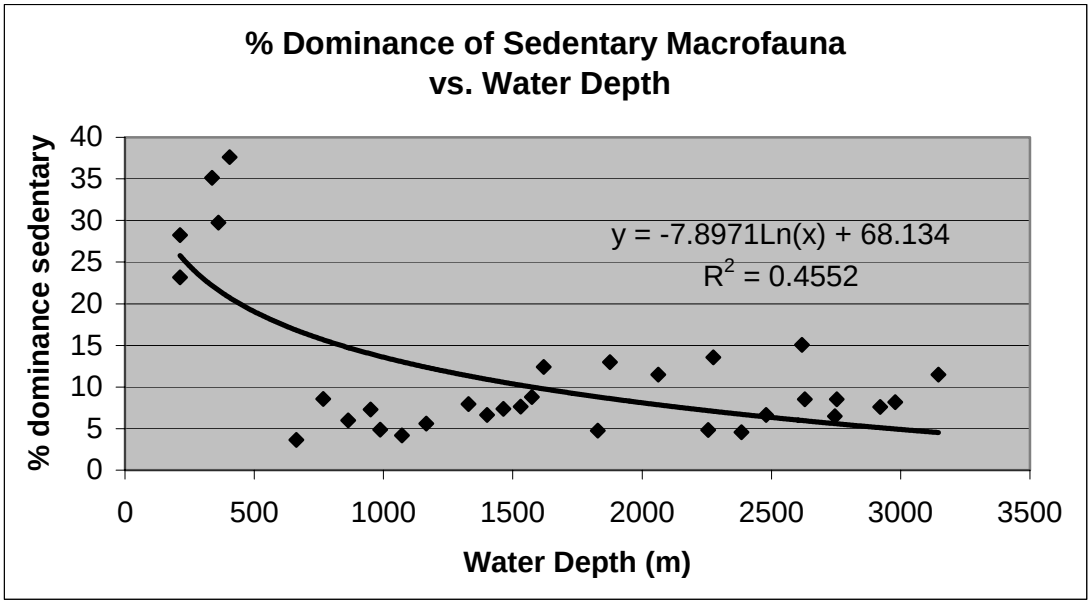

Fig. 27. Percent dominance of sedentary macrofauna in relation to water depth. High dominance values are only seen in depths shallower than 500 m. Regression used is logarithmic.

There was no statistically significant correlation to sedentary dominance vs. sediment type (Fig. 28). However, it may be noted that four of the five sites possessing the coarsest sediments (>30% sand) had relatively high dominance (>10%) of sedentary macrofauna. Station W1, which sampled the highest dominance of sedentary fauna (38%), was one of these coarse-sediment sites.

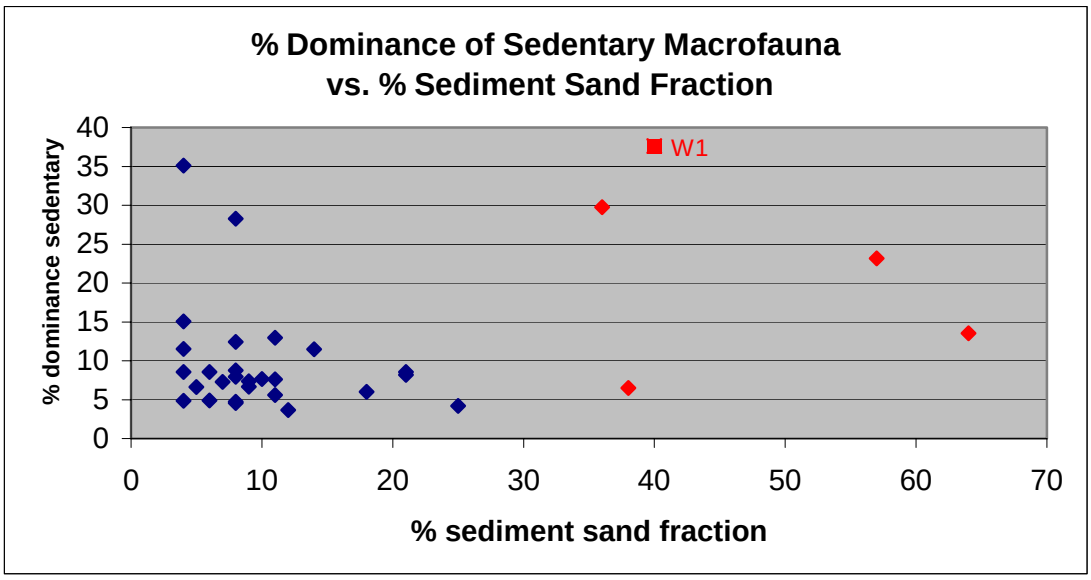

Fig. 28. Percent dominance of sedentary macrofauna in relation to percent sediment sand fraction. Points in red denote coarse sediments (>30% sand). Only one coarse sediment station (station W1) was located in the western GoM (square icon).

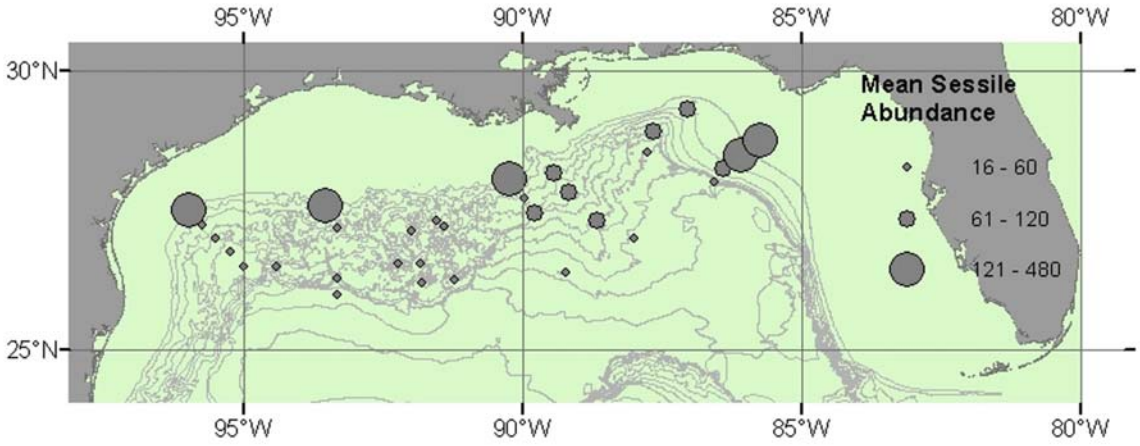

Fig. 29. Mean sedentary macrofaunal abundance patterns. Numbers are for actual sample area (.1725 m^2). The higher-range sites on the uppermost continental slope are the same ones also seen to possess high faunal percentages of sedentary macrofauna.

Mean sedentary macrofaunal *abundance* (Fig. 29) closely paralleled dominance (Fig. 26). High values (>1,500 m^2) were always present in shallower stations (<500 meters) throughout the northern GoM, with the highest density (2,779 m^2) at station W1 in the western GoM at 405 meters depth (W1 also had the highest sedentary percent dominance value, 38%).

Unlike dominance percentages, sedentary macrofaunal abundance was *not* lowest within submarine canyons or the eastern GoM. On the contrary, mean abundance values were lowest in the deep western GoM. The lowest value overall (95 m^2) was at the bottom of the Mississippi Canyon. Both the DeSoto and Mississippi Canyon sampled moderately high (>340 m^2) sedentary fauna abundances, except at the deeper margins of the continental slope. The single Alaminos Canyon station (AC1) was located on the lower slope (2,478 m), and also sampled a low abundance (110 m^2) of sedentary macrofauna.

Gulf-wide patterns of sedentary macrofauna abundance loosely mirrored that of total macrofaunal abundance, in that higher values tended to occur in shallower waters and within submarine canyons. The linear relationship between sedentary and total macrofauna abundances is shown in Fig. 17. However, sedentary macrofauna displayed a far steeper abundance decline with depth. The difference in faunal densities above and below the 500 meter upper continental slope is particularly striking (Fig. 30).

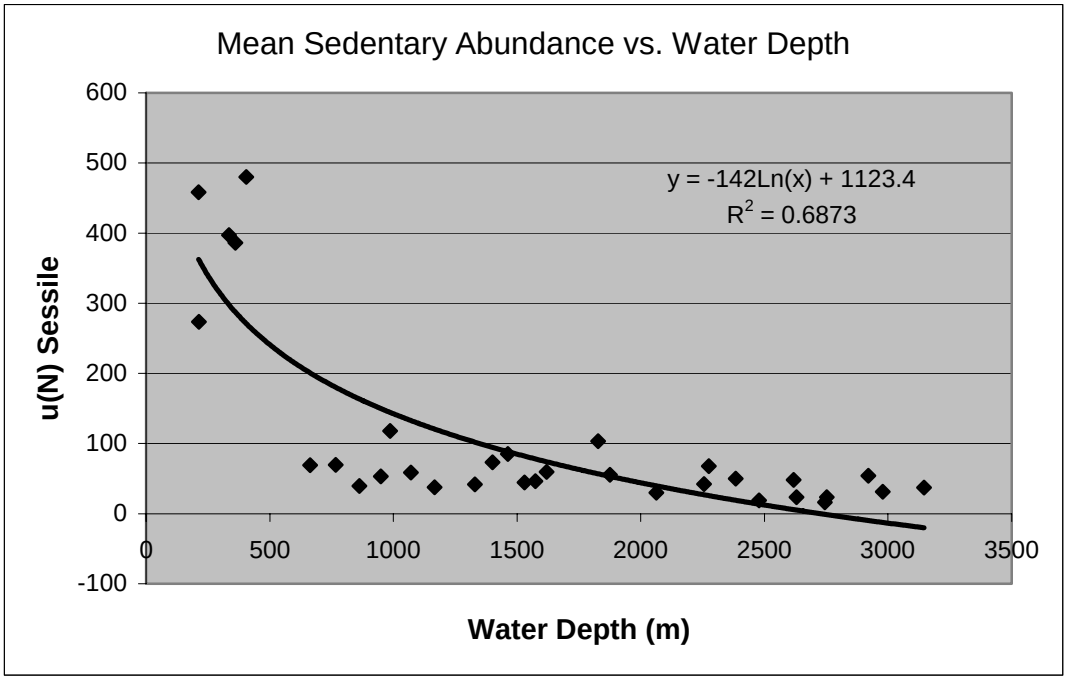

Fig. 30. Mean sedentary macrofaunal abundance in relation to water depth. Abundance values are actual (.1725 m^2). Regression used is logarithmic. Note steep decline in density below 500 meters, and similar (low) abundance patterns at mid-lower slope depths.

Significant regressional relationships for sedentary macrofauna abundance are shown in Table 10. A weak (r^2 =0.23) negative relationship was determined for within-site patchiness of taxa (beta), while a stronger (r^2 =0.34) positive relationship was found with POC (Fig. 31). It is interesting to note that four out of the five high sedentary abundance sites contained high bottom-water POC values greater than 4 uM (Fig. 32).

Table 10
Significant (>0.20) linear regressional relationships to mean sedentary abundance (LOG_{10}).

Test Variable	linear r^2
Total Mean Abundance	0.52*
Water Depth	-0.58
Taxonomic Patchiness (*beta*)	-0.23
POC	0.34*
Mean Polychaete Abundance	0.53*

* Both variables LOG_{10} transformed

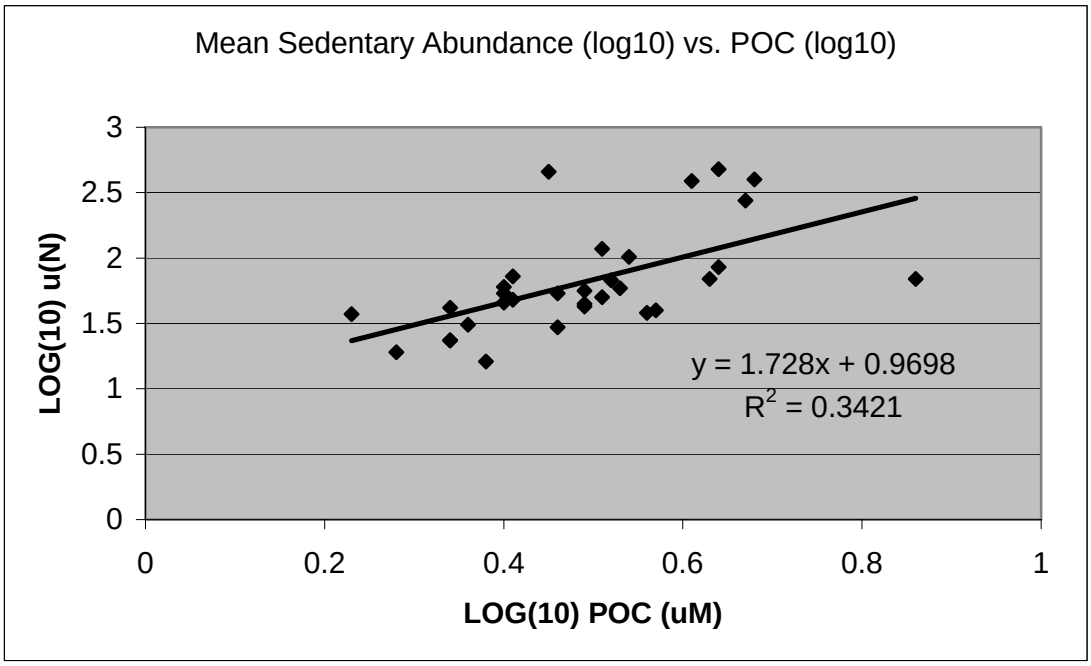

Fig. 31. Mean sedentary abundance in relation to bottom-water POC (LOG_{10}). Sedentary fauna values are LOG_{10}-transformed.

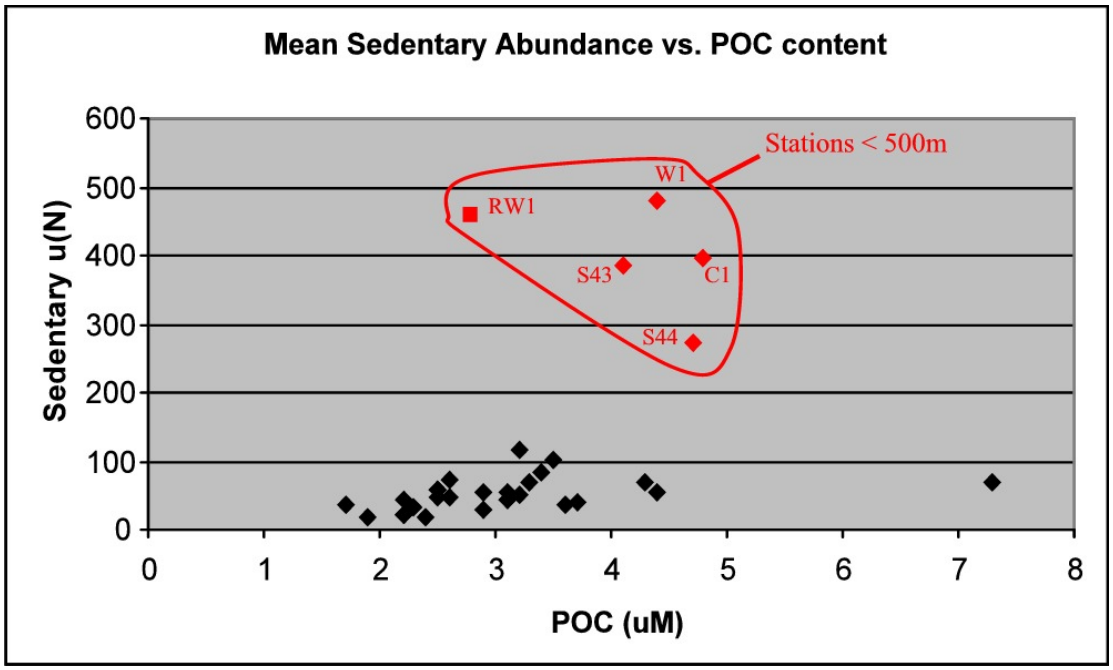

Fig. 32. Mean sedentary abundance in relation to bottom-water POC. Both POC and abundance values are actual. Note 80% of high faunal abundance values (marked in red) occur at POC levels between 4-5 uM. The exception is far western GoM station RW1 (square symbol). All high abundance values are confined to the five shallowest sites. All low sedentary abundance sites are in depths greater than 500 m.

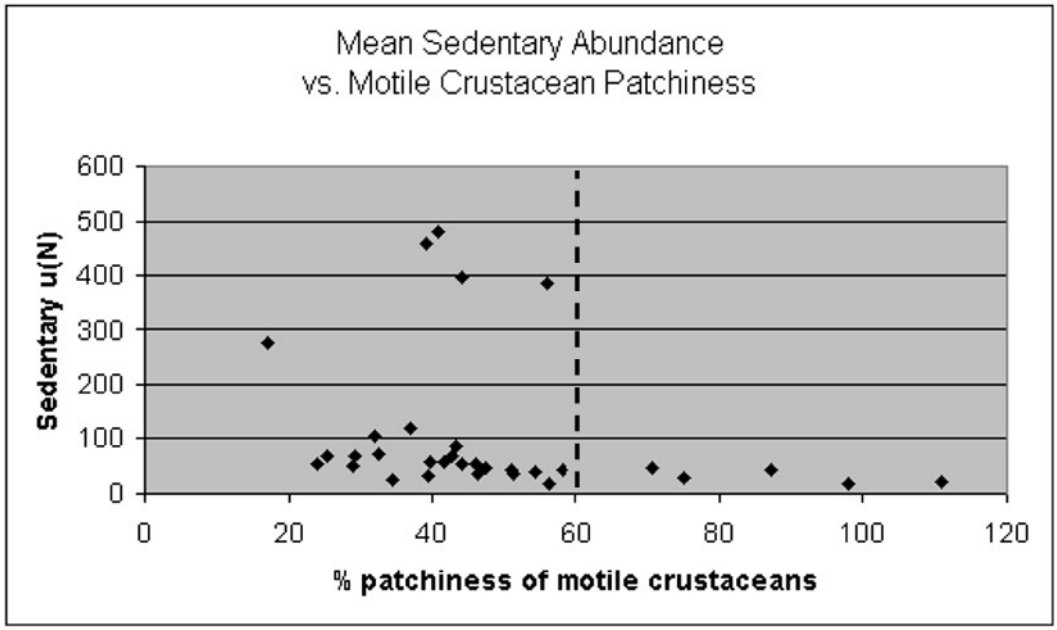

Fig. 33. Mean sedentary faunal abundance in relation to within-site abundance patchiness (c.v.) of motile crustaceans. Note that all five high-abundance sites possess crustacean patchiness less than 60%.

Sedentary macrofaunal abundance was determined not to be statistically significant in relation to sediment type, burrowing intensity, and taxonomic metadiversity. It is interesting to note (yet not statistically significant) that areas with very high sedentary abundance all had motile crustacean patchiness values under 60% (Fig. 33). Something similar was seen with polychaete abundances (Fig. 24).

3.2.2.1. Local-scale Sedentary Fauna Abundance Patchiness

Within-site abundance patchiness for sedentary macrofauna was measured using its coefficient of variance (c.v.), reported as a percentage (Fig. 34).

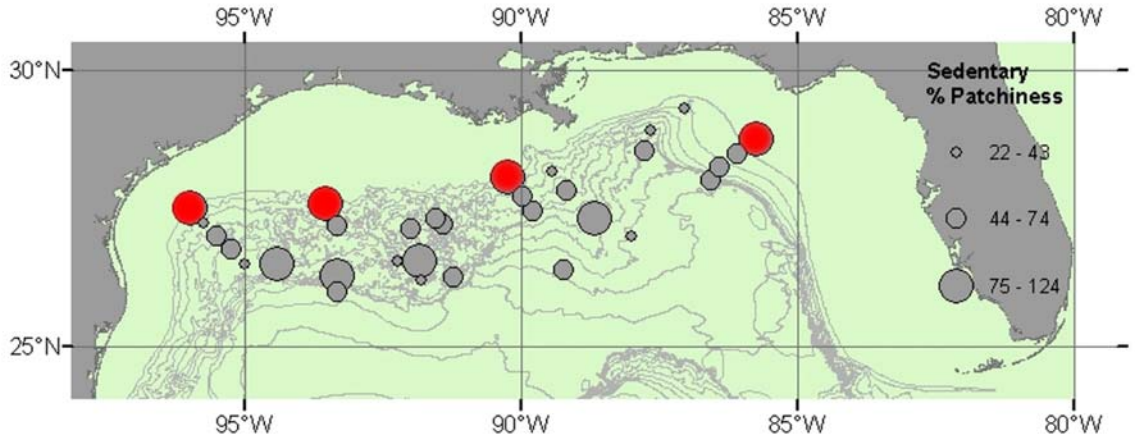

Fig. 34. Within-site patchiness of sedentary macrofauna abundance. Values are computed as coefficients of variance (c.v.), which are expressed as percentages. Note high values at same shallow water sites (indicated in red) that recorded among highest mean sedentary fauna abundance values.

Sedentary macrofaunal abundance patchiness (c.v.) displayed a weak (r^2 =0.30) linear relation with motile crustacean dominance. This is illustrated and described in Fig. 35. Overall, patchiness of sedentary macrofauna was quite high (>44%) gulf-wide, with little discernible pattern by depth or location. What *is* noticeable is very high (>75%) patchiness at four of the five shallow water sites in which very high mean abundance was measured (Fig. 29). The fifth site (station S44, 361 m depth, Florida Escarpment) measured a 74% patchiness value, which was still among one of the higher values reported. The mean value for sedentary macrofauna patchiness was 60%.

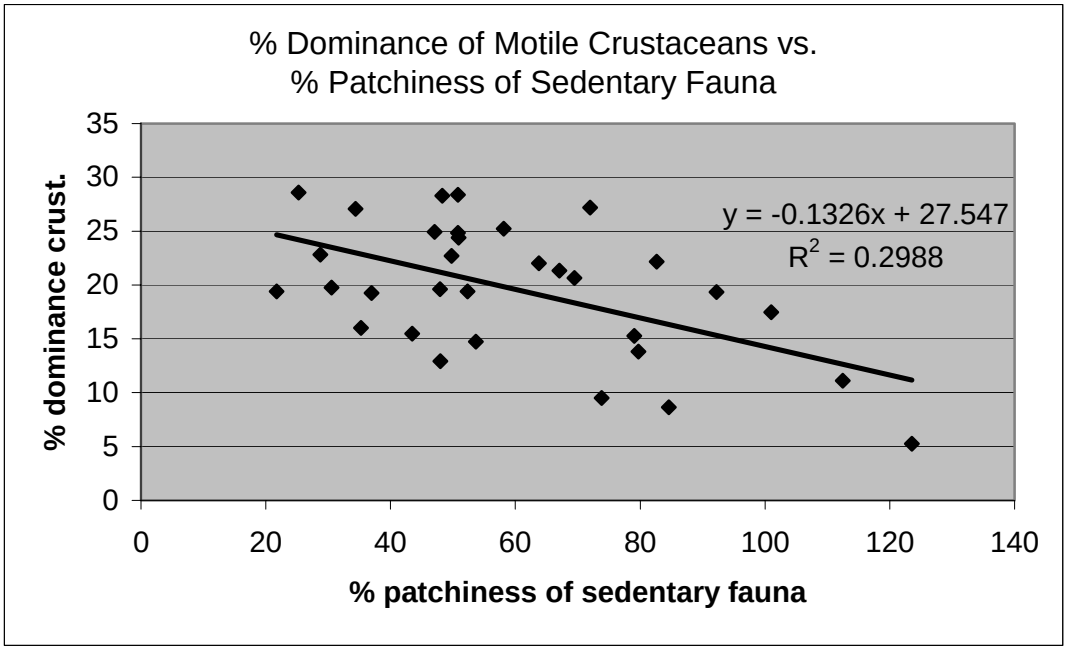

Fig. 35. Within-site abundance patchiness of sedentary macrofauna in relation to abundance percentage (% dominance) of motile crustacean macrofauna. The plot illustrates a trend whereby there is greater local-scale population homogeneity of sedentary fauna when motile crustaceans make up larger percentages of the total macrofauna.

3.2.3. Mean Motile Crustacean Abundance Patterns

"Motile crustaceans" describes a group of six macrofaunal crustacean taxa that tend to be common and easily identified (Table 6). Members of these taxa tend to be active interstitial burrowers or epibenthic crawlers. Scavenging and selective particle feeding are believed to be the predominant trophic lifestyles. These organisms are described in Methods.

The motile crustacean grouping constituted, on average, 19% of the total macrofauna sampled. Fig. 36 shows percent dominance of motile crustacean macrofauna for the northern GoM.

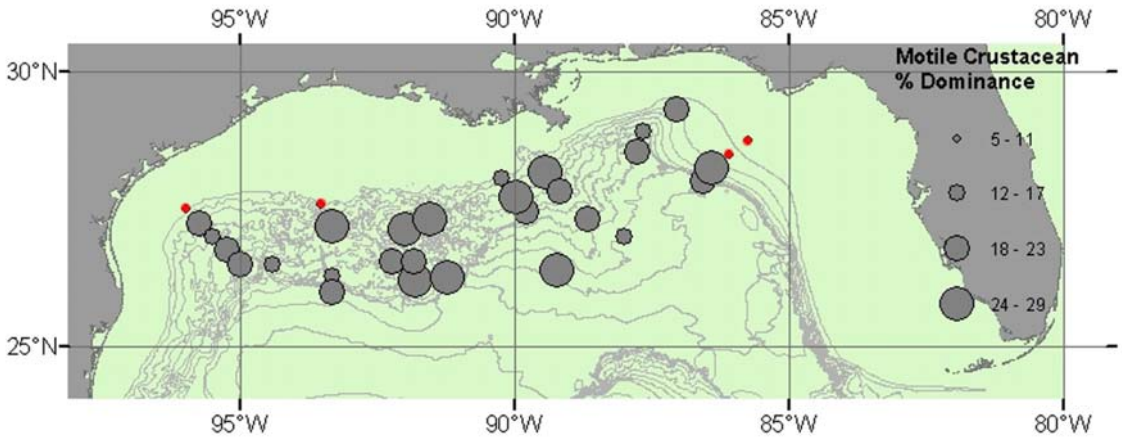

Fig. 36. Macrofaunal percent dominance of motile crustaceans. Lowest values (indicated in red) are all in shallow waters less than 500 m. This is an inverse to the pattern seen with sedentary fauna abundance, dominance and within-site patchiness (Figs. 26, 29, 34).

Motile crustacean dominance varied significantly between sampling stations. Low values (5-11%) were only encountered at four sites, all of which were shallow (<500 m) and scattered throughout the eastern and western GoM. Submarine canyon sites all possessed moderate to high (15-29%) values, with the highest value (29%) sampled along the mid-slope of the Mississippi Canyon at station MT3.

High crustacean dominance (24-29%) was encountered at over a quarter of sample sites (9 out of 32) within the north-central and northeast GoM, at varying depths throughout the continental slope. No high dominance sites were shallower than 767 meters.

Fig. 37 illustrates motile crustacean dominance vs. water depth. All shallow (<500 m) stations possessed low (< 15%) motile crustacean ratios. A positive curvilinear relationship (r^2 =0.36) was also noted.

There was no statistically significant relationship of motile crustacean to sediment type. However, it was noted that sites with coarse sediments (>30% sand) tended to have reduced crustacean dominance (Fig. 38).

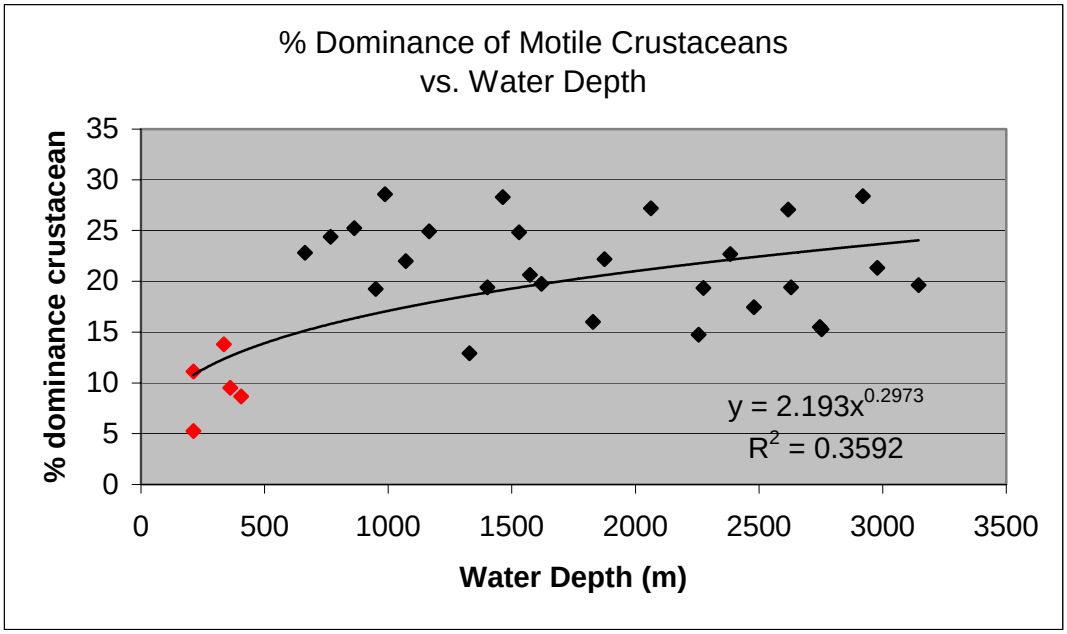

Fig. 37. Percent dominance of motile crustacean macrofauna in relation to water depth. Note low dominance values at shallowest survey stations (indicated in red). Regressional model used is power.

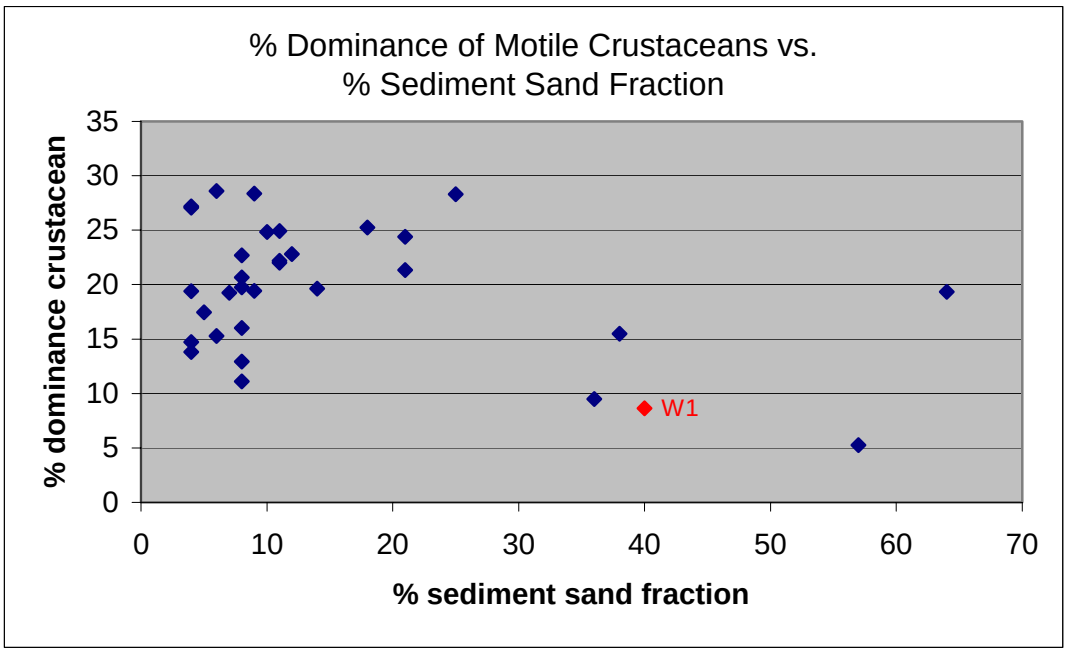

Fig. 38. Percent dominance of motile crustacean macrofauna in relation to sediment sand fraction. With the exception of station W1 (red data point), all coarse-sediment (>30% sand) sites were located in the eastern GoM.

Mean motile crustacean abundance varied from a low of 39 (226 m^2) at the bottom of the Mississippi Canyon (MT6) to a high of 691 (4,000 m^2), at the mid-slope area of the same canyon (station MT3). The average mean motile crustacean abundance throughout the deep GoM was 961 m^2. Basin-wide motile crustacean abundance patterns are shown in Fig. 39.

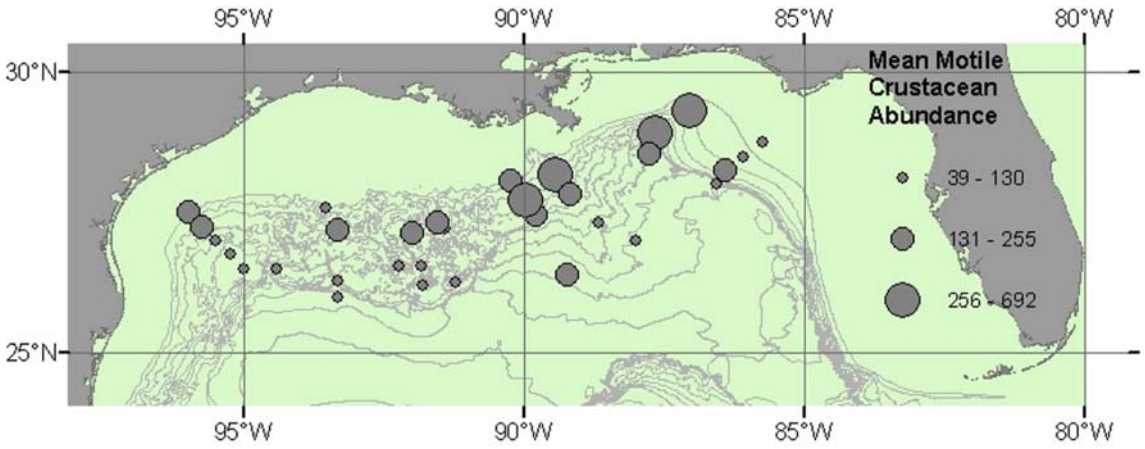

Fig. 39. Mean motile crustacean macrofaunal abundance patterns. Numbers are for actual sample area (.1725 m^2).

Unlike sedentary faunas, mean motile crustacean abundances did not parallel with abundance dominance fractions (Fig. 36). On the contrary, crustacean abundance patterns were more similar to those seen for both polychaetes (Fig. 20) and total macrofauna (Fig. 10). The biggest difference in abundance patterns between crustaceans and both polychaetes and total macrofauna is related to water depth. Whereas polychaete and total macrofauna (and even sedentary faunas) show marked declines as water depth increases (linear r^2 =0.35, 0.44 respectively), motile crustacean macrofauna show only a tenuous (linear r^2 =0.11) negative relationship (Fig. 40).

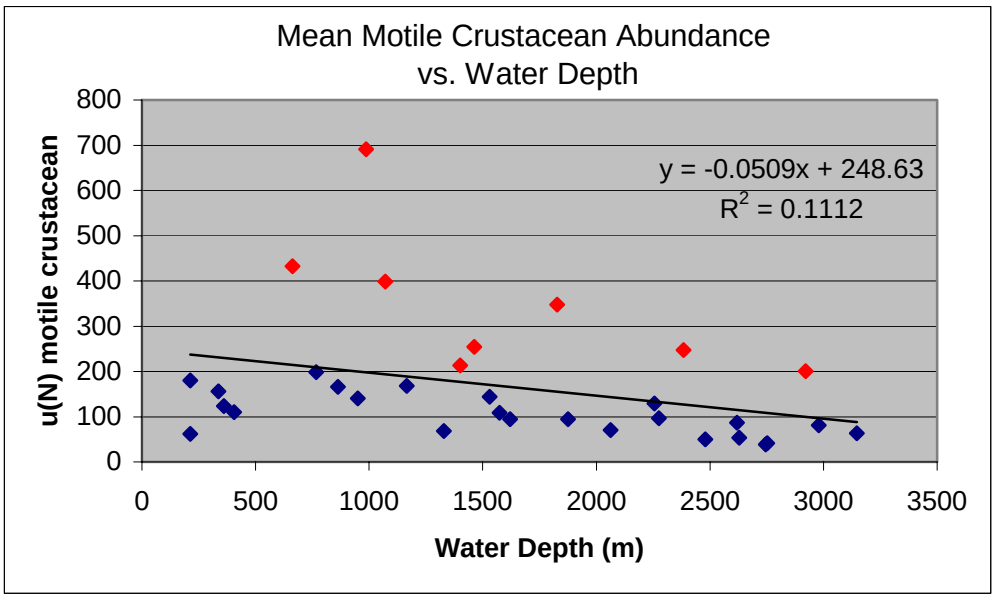

Fig. 40. Mean motile crustacean abundance in relation to water depth. High abundance sites (red) are all in the central or eastern GoM. Regression model used is linear. Motile crustacean abundance values are actual (0.1725 m^2).

Like polychaetes, motile crustacean abundance was much higher in the lower DeSoto Canyon (>1,400 m^2) than at similarly deep stations in the Alaminos and Mississippi Canyons (<580 m^2).

Station MT3 (987 m) in the upper Mississippi Canyon not only possessed the highest motile crustacean abundance from the 32 survey stations, but it was over 35% higher than the next most crustacean-abundant survey station (S35 in the upper DeSoto Canyon). Overall, the western GoM displayed lower motile crustacean abundances than the eastern and central GoM (Fig. 40).

Significant regressional relationships for motile crustacean macrofauna abundance are shown in Table 11. A weak (linear r^2 =.22) negative relationship was observed for within-site patchiness of taxa (beta), while a stronger (27%) *positive* relationship was

found with bioturbation intensity. Bottom-water POC content was also found to show a weak link (linear r^2 =0.26) to macrofaunal crustacean abundance.

Table 11
Significant (>0.20) linear regressional relationships to mean motile crustacean abundance (LOG_{10}).

Test Variable	linear r^2
Total Mean Abundance	0.71*
Mean Polychaete Abundance	0.54*
Mean Sedentary Abundance ¥	0.67*
Water Depth	-0.20
Taxonomic Patchiness (*beta*)	-0.22
Bioturbation	0.21
POC	0.26 (0.32*)

* Both variables LOG_{10}-transformed
¥ Very-high sedentary values removed

Motile crustacean macrofaunal abundance was determined not to be statistically significant in relation to sediment type. However, as seen with crustacean community dominance, areas with coarse sediments all exhibited reduced crustacean densities (Fig. 41).

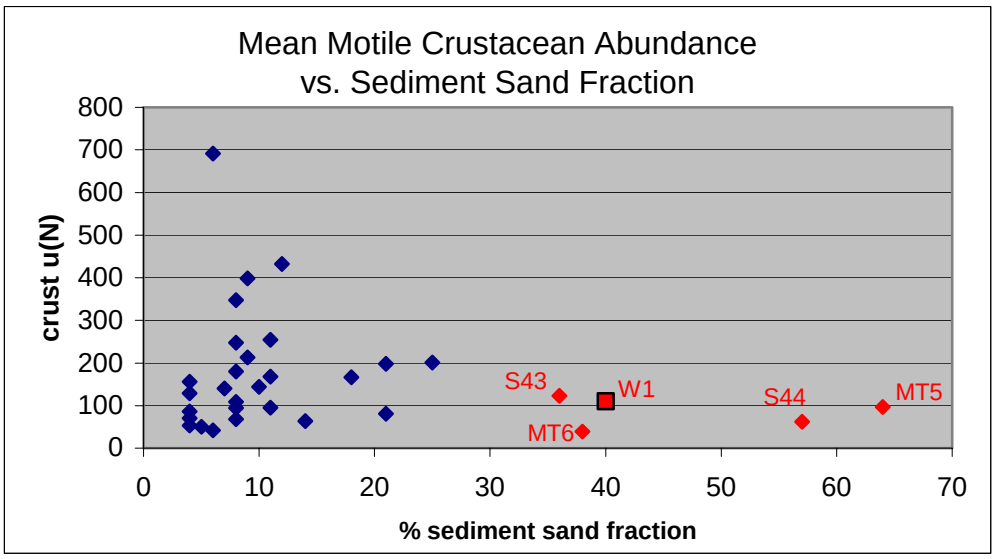

Fig. 41. Mean motile crustacean abundance in relation to sediment sand fraction. All five survey stations possessing >30% sand content (indicated in red) maintain relatively low motile crustacean densities. Station W1 (square icon) is the only western GoM station possessing a sand content >30%. Motile crustacean abundance values are actual (0.1725 m^2).

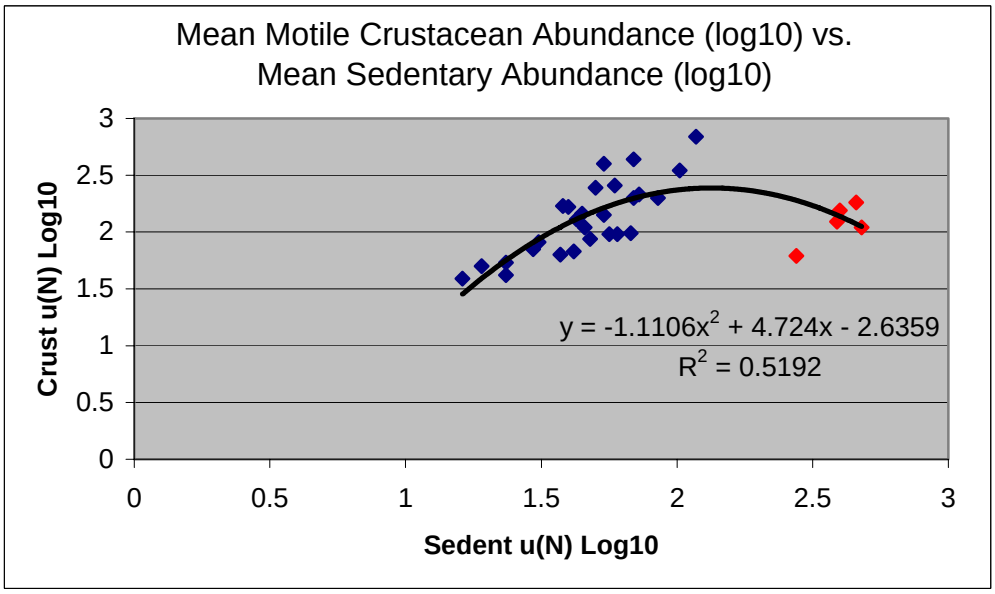

Fig. 42. Mean motile crustacean abundance in relation to mean sedentary abundance. Both values are LOG_{10}-transformed. Regression curve used is second-order polynomial. Data points in red indicate the five shallow water, very-high sedentary abundance sites.

Although only a very poor linear relationship (r^2 =0.13) was seen between motile crustaceans and sedentary fauna, a curvilinear relationship showed a more interesting pattern (Fig. 42). This would seem to point out a negative control against motile crustacean macrofauna when sedentary macrofauna are extremely abundant.

If the five shallow-water, very-high sedentary abundance survey sites (RW1, W1, C1, S44, S43) were omitted from analysis, a very strong linear relationship (r^2 =0.67) between motile crustacean and sedentary abundance is exhibited (Fig. 43).

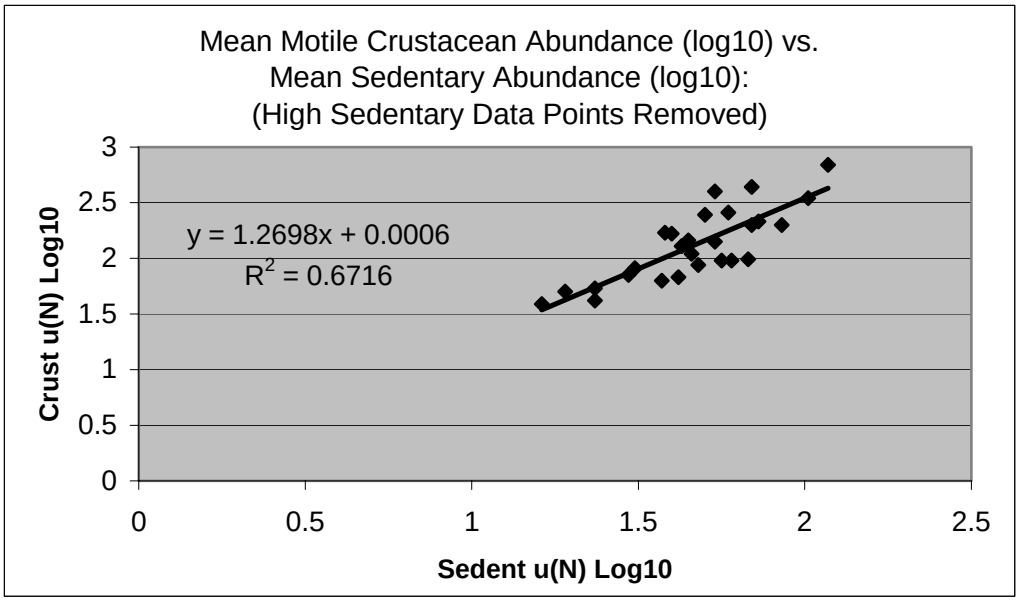

Fig. 43. Mean motile crustacean abundance in relation to mean sedentary abundance, with very high sedentary fauna abundance sites (Fig. 42) removed.

A linear relationship between crustacean abundance and taxonomic metadiversity was also very poor (r^2 =0.11), but much stronger when fitted with a model II curvilinear line (Fig. 44). Motile crustacean densities were seen to drop as diversity of other macrofaunal

groups increased, but when a high enough taxonomic diversity was reached (>8), crustacean abundance recovered somewhat.

As seen for the other macrofaunal groups, motile crustacean abundance displayed a positive relationship with bottom-water POC (Fig. 45).

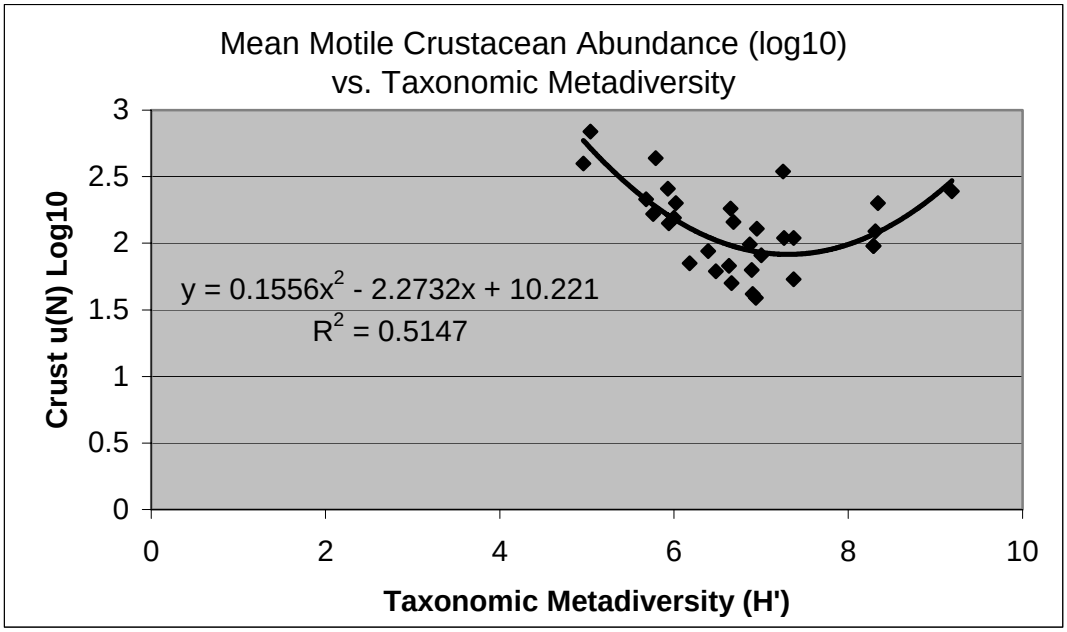

Fig. 44. Mean motile crustacean abundance in relation to taxonomic metadiversity of total macrofauna. Regression used is second-order polynomial.

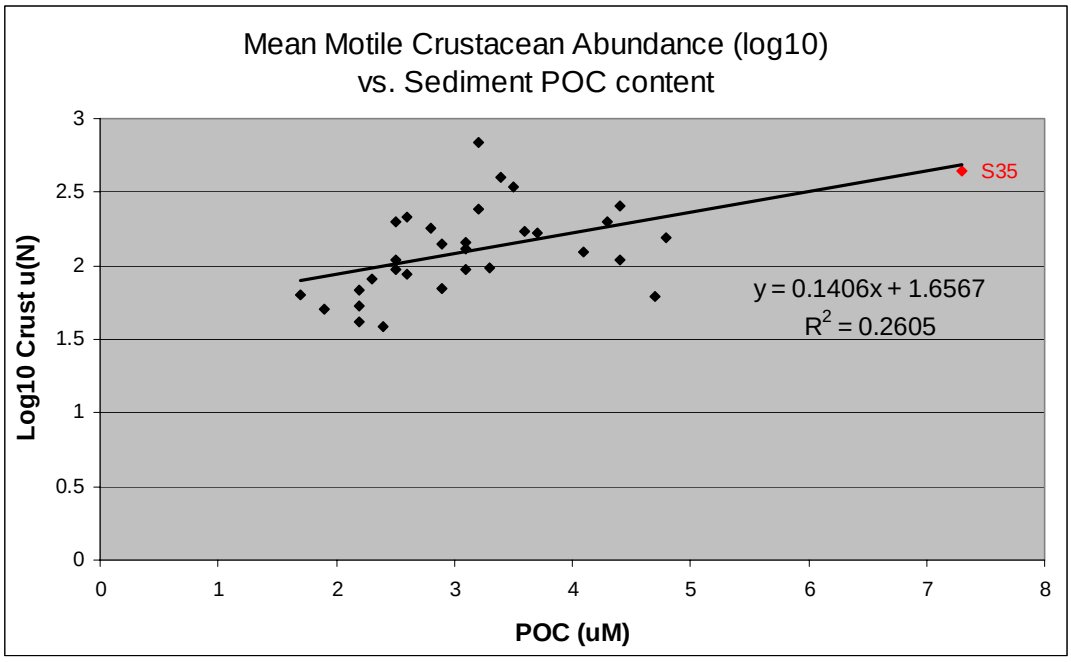

Fig. 45. Mean motile crustacean abundance (LOG_{10}) in relation to bottom-water POC content. POC values are actual. Very high POC value (7.3 uM) is from site S35 (indicated in red) at top of DeSoto canyon.

3.2.3.1. Local-scale Motile Crustacean Abundance Patchiness

Within-site abundance patchiness for motile crustacean macrofauna was measured using its coefficient of variance (c.v.), reported as a percentage (Fig. 46).

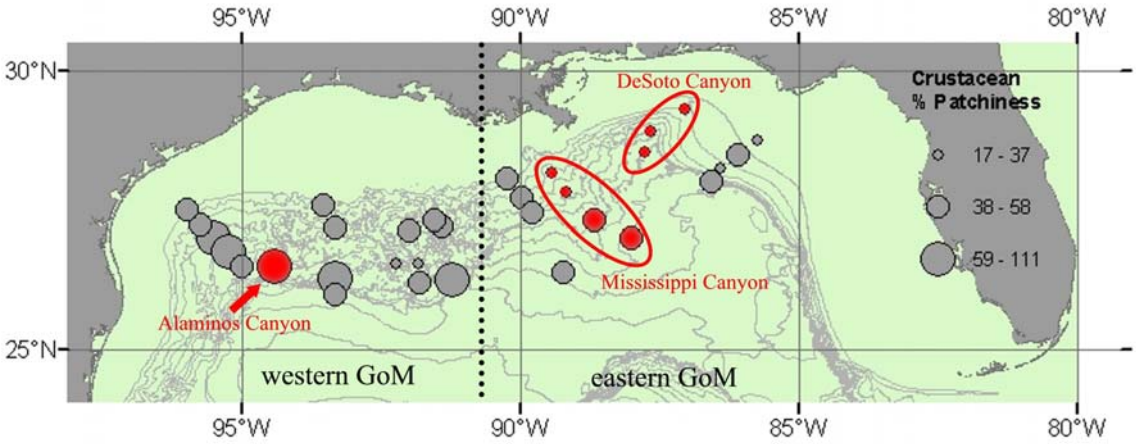

Fig. 46. Within-site patchiness of motile crustacean macrofauna abundance. Values are computed as coefficients of variance (c.v.), which are expressed as percentages. Canyon sites are marked in red. Patchiness values for motile crustaceans are higher in the western GoM than the eastern GoM.

Looking at patchiness patterns gulf-wide, it is visually evident that the DeSoto and (upper) Mississippi canyons had much lower local-scale crustacean patchiness than the Alaminos canyon site. It is also clear that the eastern GoM has much less patchiness compared to the western GoM.

Motile crustacean abundance patchiness (c.v.) displayed a negative linear regressional relationship (r^2 =0.26) to bottom-water POC (Fig. 47), and a positive linear relationship (r^2 =0.29) with taxonomic patchiness. The latter is discussed in section 3.5.

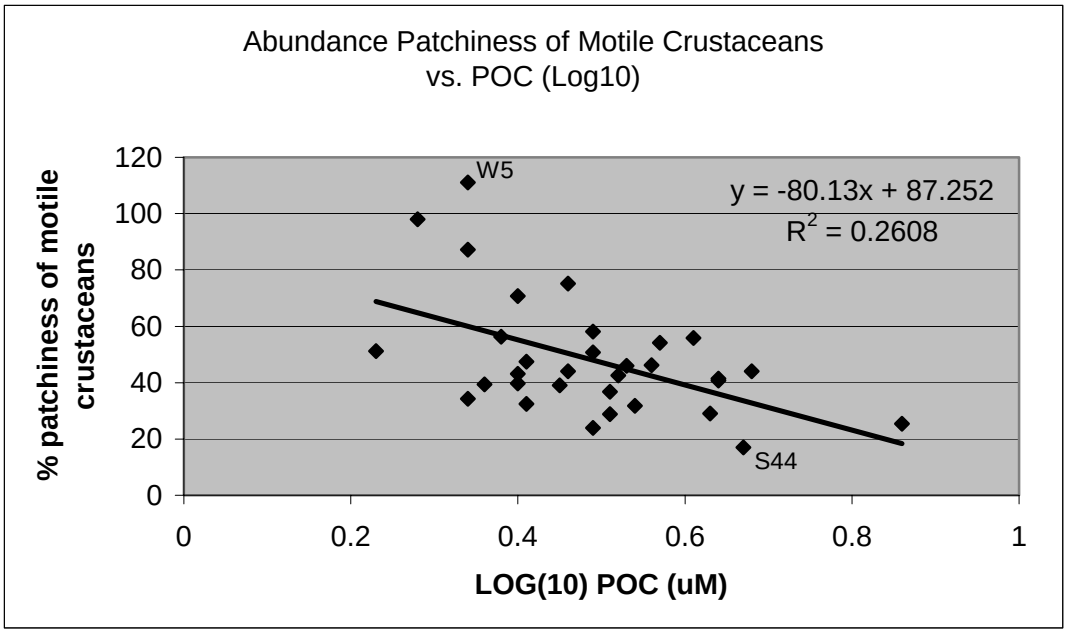

Fig. 47. Abundance patchiness (c.v.) of motile crustaceans in relation to (LOG_{10}) bottom-water POC. Highest and lowest patchiness stations are indicated.

The mean value for local-scale, motile crustacean macrofauna patchiness was 48%. The highest value (111%) was encountered in the deep western GoM at station W5 (2,753 m). The lowest value (17%) was measured at the top of the Florida Escarpment (station S44 at 213 m). Interestingly, this same site (S44) was one that measured the fifth *highest* local-scale patchiness for sedentary macrofauna. Similar but less dramatic examples were seen at other stations with very high sedentary faunal abundance. High values for local-scale crustacean patchiness and sedentary abundance were exclusive of one another (Fig. 48).

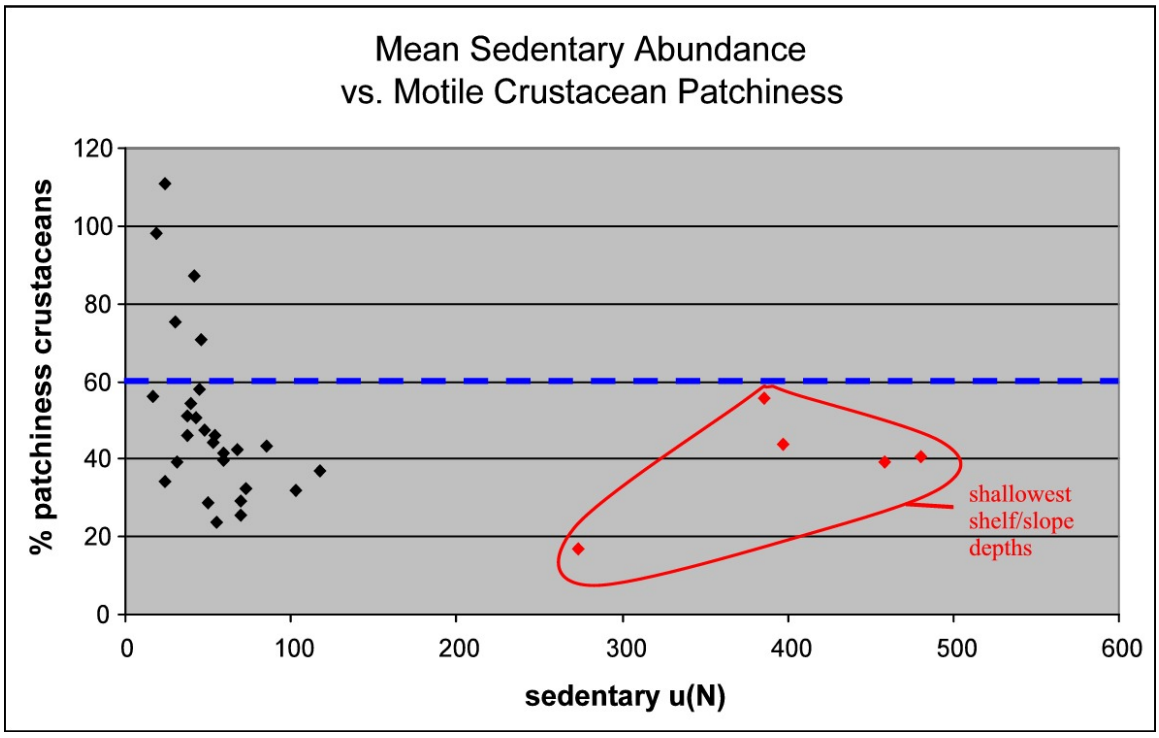

Fig. 48. Mean sedentary faunal abundance in relation to within-site abundance patchiness (c.v.) of motile crustaceans. Note that all five high-abundance sites (indicated in red) possess crustacean patchiness less than 60%. These high-abundance sites are also the five shallowest survey stations, located at the shelf/slope break.

3.3. Taxonomic Richness

A total of 43 higher invertebrate taxa were initially selected in the macrofaunal screening process (Table 5). For each survey site, both mean (between within-site samples) and pooled (combined within-site samples) measurements were collected. Taxonomic richness was not incorporated into the main statistical testing regime, as taxonomic diversity (derived from richness and abundance) was deemed more useful (richness typically being a function of sample abundance). However, some basic comparisons were made of taxonomic richness.

3.3.1. Pooled Taxonomic Richness (five within-site samples combined)

Between 22-36 (51-84%) of the 43 screened macrofaunal taxa were encountered at each survey station. The average richness value Gulf-wide was 30 taxa, or roughly two-thirds of the screened macrofaunal groups. Higher (32 taxa) pooled taxonomic richness did not show a clear correlation with water depth (Fig. 49).

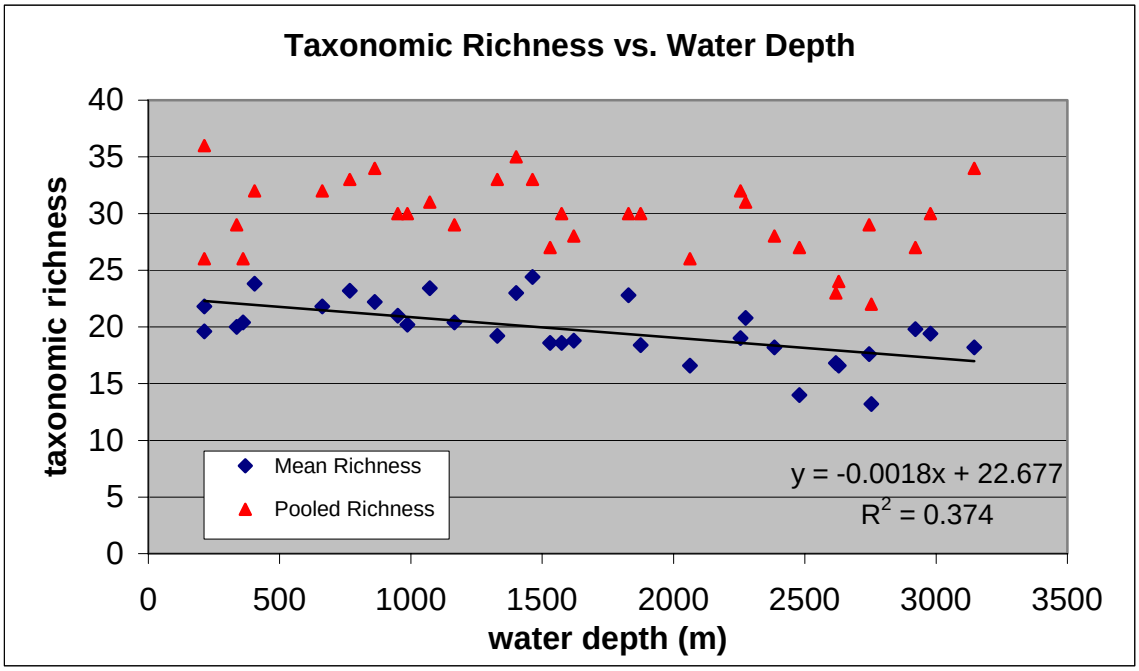

Fig. 49. Taxonomic richness in relation to water depth. Both pooled and mean richness values are shown. Mean richness generally drops with depth (indicated by regression line), while pooled richness does not.

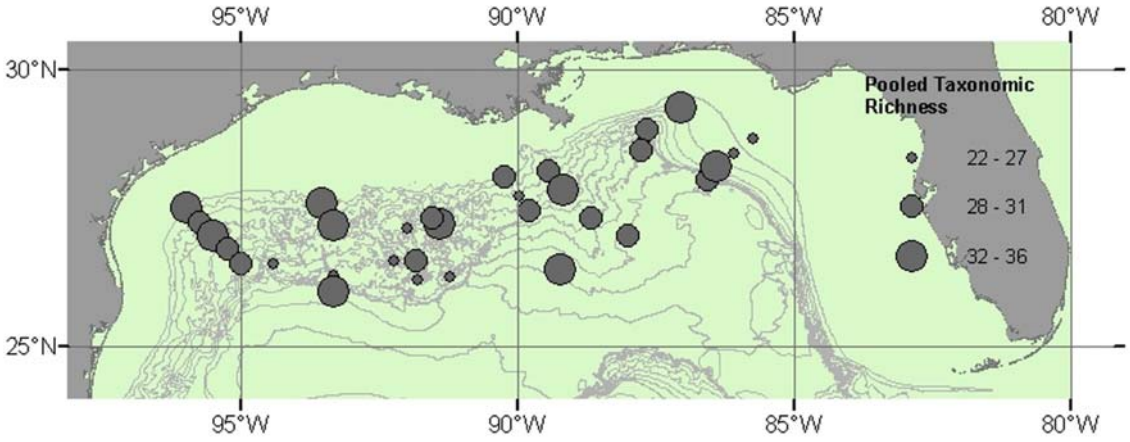

Fig. 50. Pooled macrofaunal taxonomic richness values. Taxonomic richness for each site is measured by combining all five boxcore subsamples.

The highest pooled value (36 taxa) was seen at station RW1 (213 m) in the far western GoM. Other high-value areas were found throughout all sampling depths, throughout the GoM sampling area (Fig. 50).

Unlike higher pooled richness values (32-36 taxa), low pooled richness values (22-27 taxa) tended to be found at deeper slope depths (>2,000 m), though very shallow exceptions existed on the Florida Escarpment. The lowest pooled value (22 taxa) was measured at station W5 (2,753 m) in the western GoM. Other low-richness sites were seen at deep basin sites B3 (2,618 m, 23 taxa) and B2 (2,629 m, 24 taxa). A third deep basin site (B1, 2,255 m) possessed much higher richness (32 taxa).

3.3.2. Mean Taxonomic Richness (average of five within-site samples)

Averaged from five individual subsamples taken at each survey station, 13-24 (30-56%) of the 43 macrofaunal screening taxa were encountered. Higher (21-24 taxa)

taxonomic richness was generally measured at mid-upper slope depths <1,500 m (there was one exception at 1,828 m, within the DeSoto Canyon), with the highest mean value (24.4 taxa) occurring at station C4 (1,463 m) in the north-central GoM (Fig. 51).

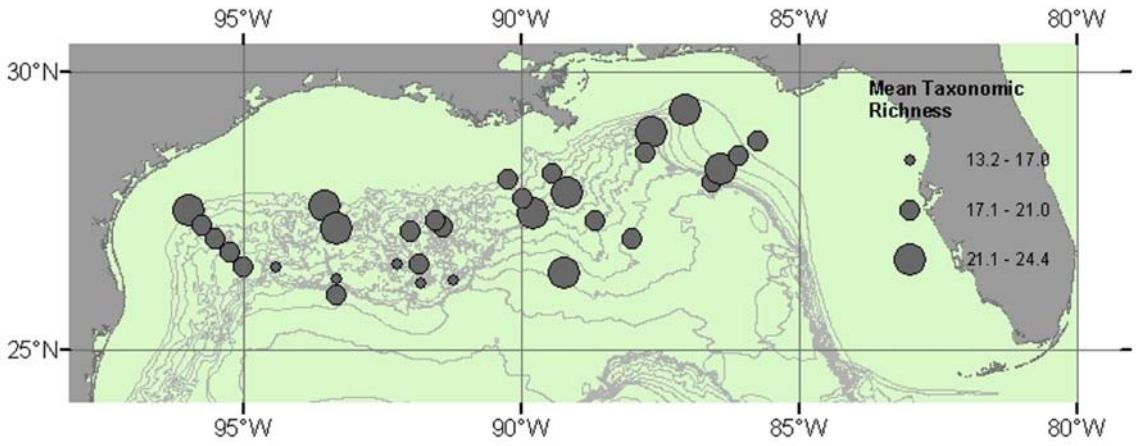

Fig. 51. Mean macrofaunal taxonomic richness values. Taxonomic richness for each site is calculated from the mean richness value between the five within-site subsamples.

The lowest mean richness measurements (13-17 taxa) were all found along lower slope depths (>2,000 m), with the lowest mean value (13.2 taxa) occurring at station W5 (2,753 m) in the western GoM. This site also possessed the lowest pooled taxonomic richness (22 taxa).

Other than water depth (Fig. 49), only one other test variable (near-bottom POC) displayed a pattern with taxonomic richness. This is discussed further in section 3.9.

3.4. Taxonomic Metadiversity

Higher taxonomic diversity (shortened to “metadiversity” for this study) was calculated using the Shannon-Weiner (LOG_{10}) function, substituting values for species

richness with those of taxonomic richness. This is more thoroughly explained in the Methods section. One of the key constraints in using higher order taxa in lieu of genera or species is that the theoretical maximum of higher taxa that could be encountered was capped at 43, and the *realized* maximum for any specific boxcore sample was 28 macrofaunal groups. Thus, richness values had a fixed maximum designated by the DGoMB program design. Another major drawback is that use of higher order taxa as discrete variables is arguably more subjective than that for lower order taxa (particularly genus and species level). This is discussed in section 5.6.

Metadiversity measurements varied between a low of 4.96 (station C7, 1,072 m), to a high of 9.19 (station S37, 2,384 m). The basin-wide average was 6.77. Taxonomic metadiversity patterns throughout the sampling area are illustrated in Fig. 52.

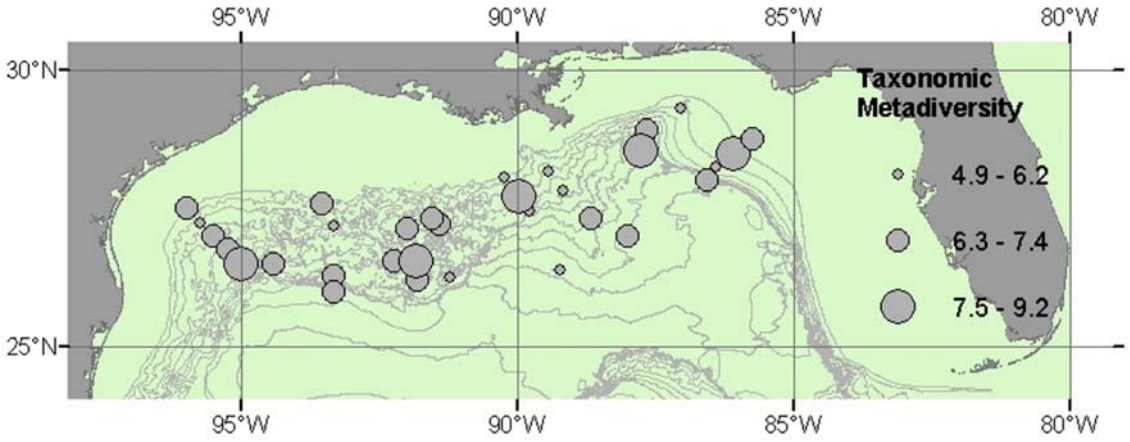

Fig. 52. Higher taxonomic diversity patterns throughout the GoM. There do not appear to be any distinct geographic correlatives.

No statistically significant relationships were discovered between taxonomic metadiversity and other test variables. Even water depth did not appear linked (Fig. 53).

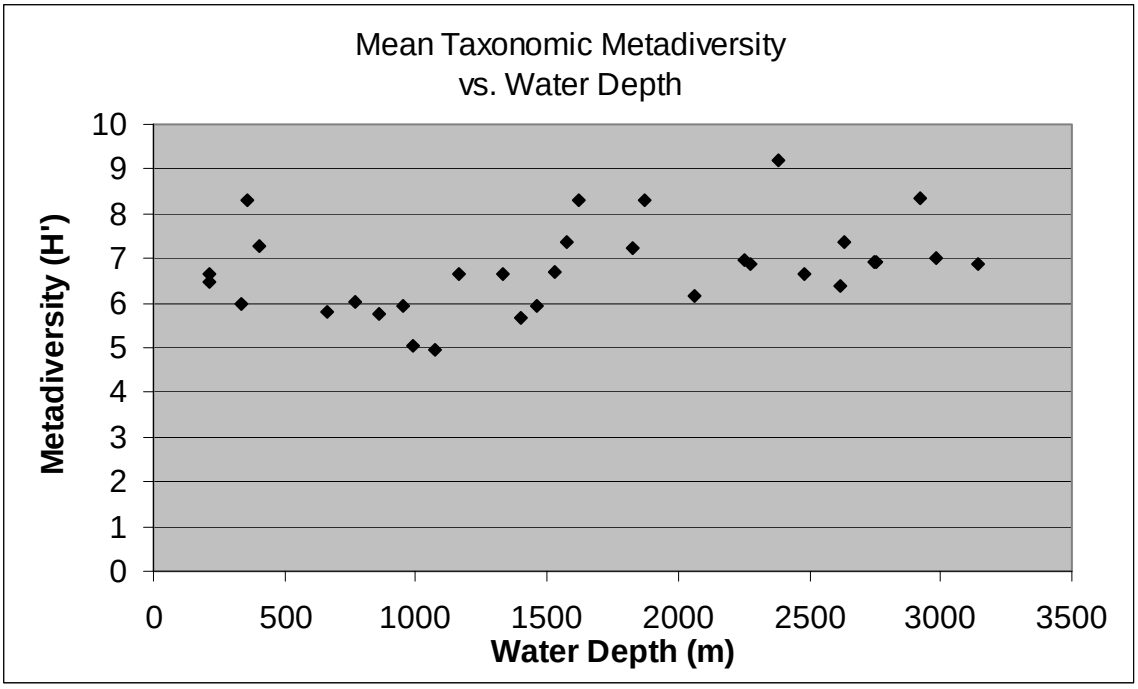

Fig. 53. Mean taxonomic metadiversity in relation to water depth. There is no statistically significant relationship (regressional r^2 <0.13; ANOVA F-value >0.05).

3.5. Taxonomic Within-Site Patchiness (*beta*)

Local-scale community heterogeneity of macrofauna was measured by calculating *beta* (turnover) diversity from both pooled and mean taxonomic richness values. High *beta* values indicate less taxa-level commonality between station subsamples, which indicates patchiness at the local level. A *beta* of 1.0 implies complete commonality (no patchiness of taxa types), while a value of 2.0 indicates 50% patchiness, 3.0 is 67%, 4.0 is 75%, etc…

Taxonomic intra-site patchiness values for the GoM varied between 1.27-1.93, equating to percentage patchiness values of 21-48%. The mean local intra-site patchiness was 1.51 (34%).

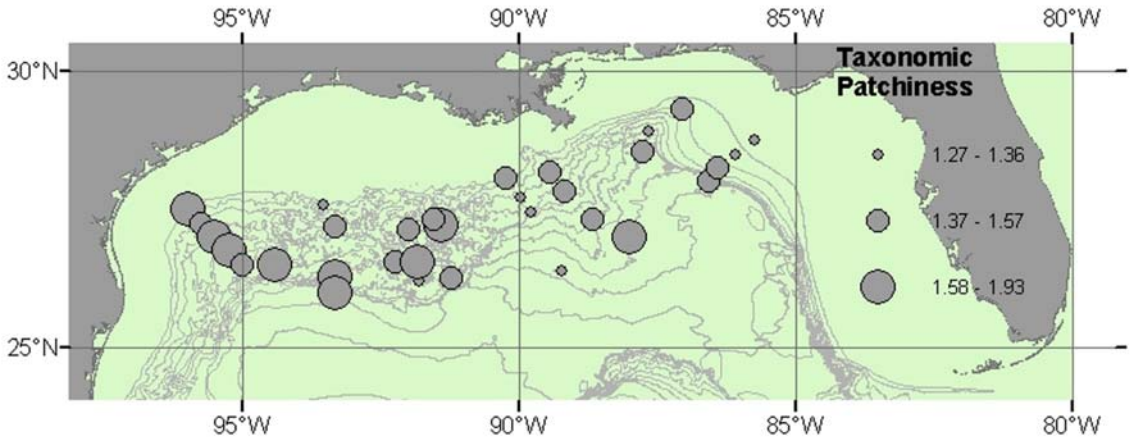

Fig. 54. Macrofaunal within-site patchiness (beta) values of higher taxa. The western GoM contains higher local-scale, intra-site patchiness than the eastern GoM. High patchiness areas also appear to be absent from almost all shallow water sample sites.

Lower (1.27-1.37) measurements of taxonomic *beta* were encountered at eight survey sites. Most of these (6) were in the central or eastern GoM (Fig. 54); all were at varying depths from the shelf break to the lower slope. The lowest measurement (1.27) was taken at station S43 (361 m) on the upper Florida Escarpment.

High *beta* measurements occurred between values of 1.58-1.93, encompassing nine survey stations. Except for a single deep site in the lower Mississippi Canyon (MT6, 2,745 m), high-patchiness sites were all relegated to the west and west-central GoM. Eight of the nine high-patchiness sites were located mid-lower slope depths greater than

1,500 m; the exception was RW1 (213 m) in the far western GoM. The survey site with the highest taxonomic *beta* (1.93, 48%) was within the Alaminos Canyon.

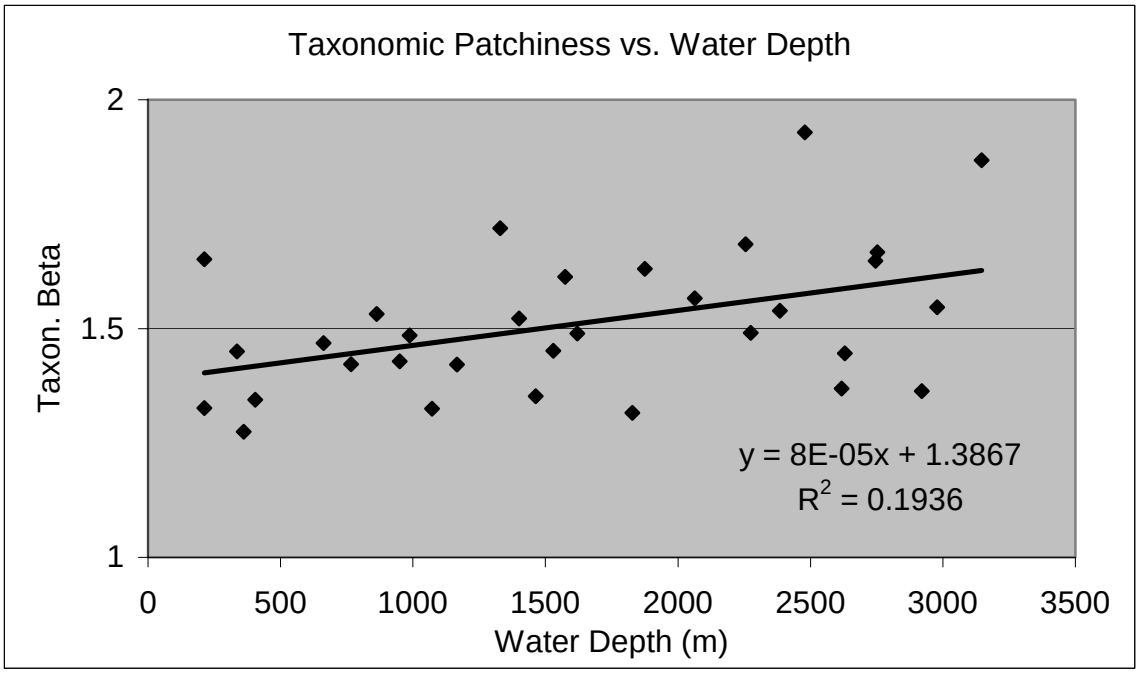

Fig. 55. Taxonomic patchiness (*beta*) patterns in relation to water depth.

There was only a very weak (r^2 =0.19) linear relationship of taxonomic patchiness with water depth (Fig. 55). It is possible that higher patchiness at deeper depths is somewhat linked to the reduced macrofaunal abundance and taxonomic richness also generally found there (Figs. 8, 11). It is also possible that the patchiness to water depth trend is related to the imprecision of the GOMEX boxcorer (described in Methods). This greater dispersion may account for the higher intra-site patchiness values seen at many deepwater survey stations.

Statistically significant relationships to local-scale taxonomic patchiness of macrofauna are shown in Table 12.

Table 12
Significant (>0.20) linear regressional relationships to macrofaunal taxonomic patchiness (*beta*).

Test Variable	linear r^2
POC	-0.28 (-0.39*)
Sediment Clay Fraction	0.22
Total Mean Abundance	-0.27*
Mean Polychaete Abundance	-0.24*
Mean Sedentary Abundance	-0.23*
Mean Motile Crustacean Abundance	-0.22*
Motile Crustacean Within-Site Abundance Patchiness (c.v.)	0.29

* Independent variable LOG_{10} transformed

Taxonomic patchiness had the highest relationship to bottom-water POC (Figs. 56). When fitted with a curvilinear regression line (Fig. 57) and LOG_{10}-transformed (Fig. 58), much stronger patterns (r^2 >0.50) were noted. Areas with higher bottom-water POC concentrations tended towards having a greater taxonomic homogeneity, while more patchy distribution of local taxa was measured at stations with low POC content. The two stations possessing the lowest POC values were AC1 (Alaminos Canyon, 2,479 m) and W6 (deep western GoM, 3,146 m) also contained the most patchy macrofaunal taxa dispersion (Fig. 56).

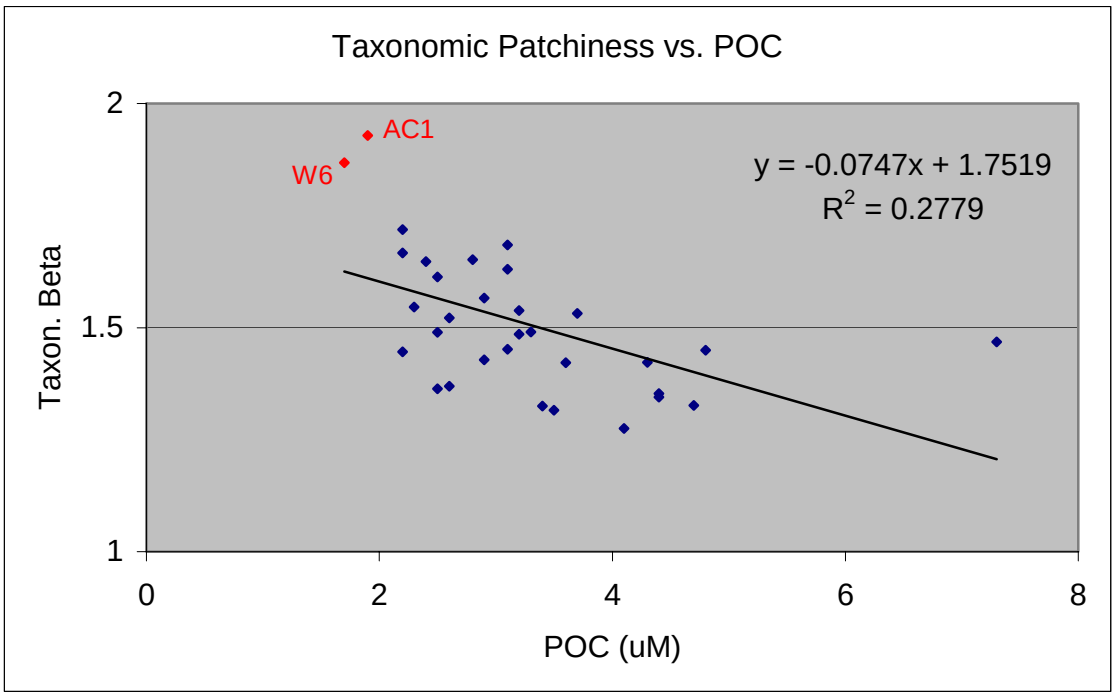

Fig. 56. Taxonomic patchiness in relation to bottom-water POC. POC values are actual. Values in red indicate Alaminos canyon (AC1) and deep western GoM (W6) survey stations.

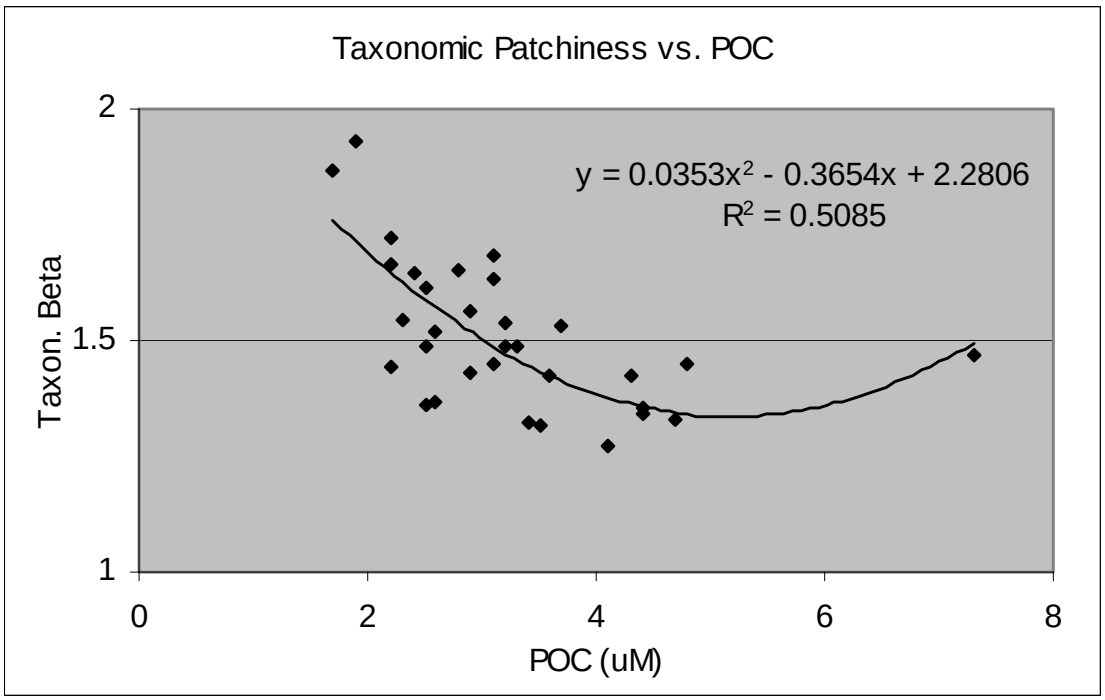

Fig. 57. Taxonomic patchiness in relation to bottom-water POC, fitted with a second-order polynomial regression line.

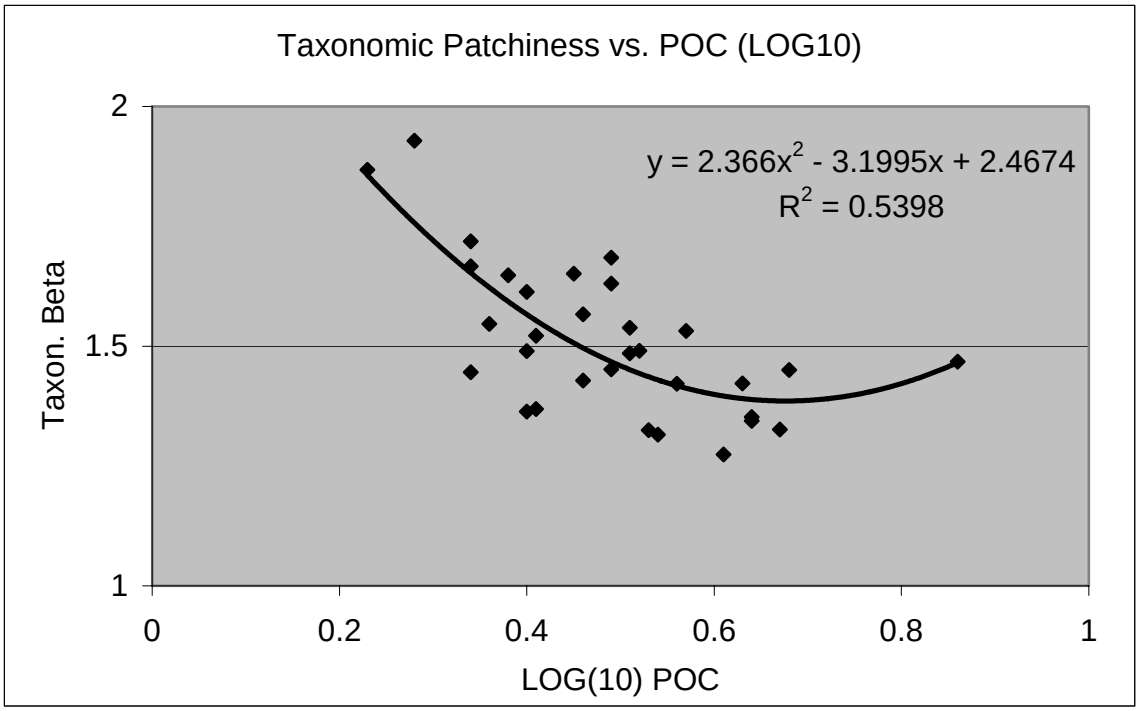

Fig. 58. Taxonomic patchiness in relation to (LOG_{10}) bottom-water POC. Regression line used is second-order polynomial.

The majority of DGoMB survey stations contained surface sediment clay percentages in excess of 40%. These high-clay areas did not appear depth-related. There was a weak curvilinear relationship (r^2 =0.26) between clay content and local taxonomic patchiness (Fig. 59). For total mean macrofaunal, mean polychaete, mean sedentary, and mean motile crustacean abundances, there were weak (linear r^2 values between 0.22-0.29) negative relationships with taxonomic patchiness. This is illustrated for total mean macrofaunal abundance in Fig. 11; the relationship is similar for polychaetes, sedentary fauna, and motile crustaceans (Table 12). Within-site abundance patchiness for motile crustacean macrofauna displayed the highest (linear r^2 =0.29) faunal abundance

relationship to local taxonomic patchiness (Fig. 60). Put another way, this might indicate that the more homogeneous the local-scale densities of crustacean macrofauna, the more homogeneous is the local-scale taxonomic diversity overall.

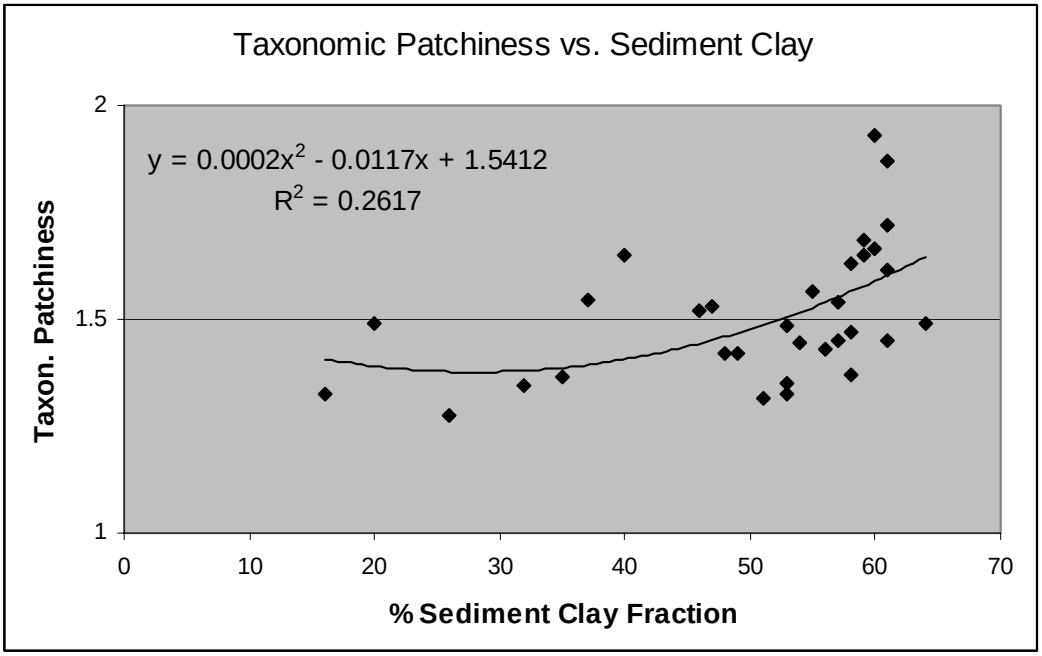

Fig. 59. Taxonomic patchiness in relation to sediment clay content. There is a weak positive relationship. Excluding low-clay (<40%) areas from the regression (not shown) only marginally improved the relationship (r^2 =0.31). Regression model used is second-order polynomial.

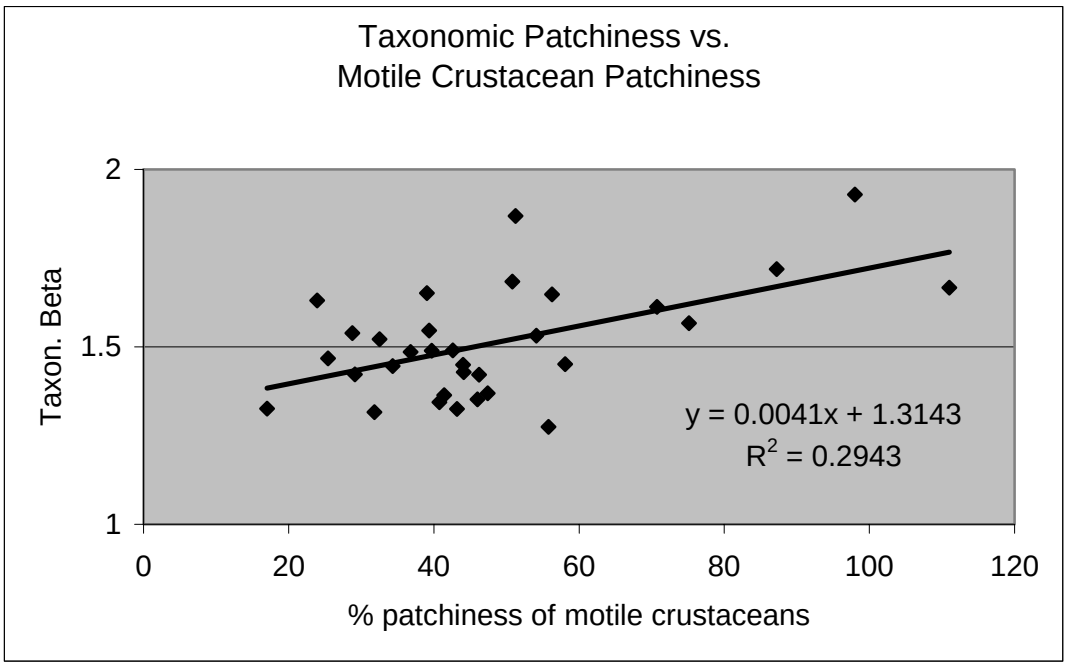

Fig. 60. Taxonomic patchiness in relation to within-site abundance patchiness (c.v) of motile crustaceans.

3.6. Seafloor Bioturbation: Megafaunal Burrowing Intensity

Small-scale habitat heterogeneity, and sediment burrowing disturbance of the seafloor was measured by evaluating bottom photographs for the presence/absence of megafaunal-derived surface relief in the form of mounds and burrows. The specific protocols are outlined in Methods. Megafaunal bioturbation was ranked into five separate categories (Table 13).

Table 13
Site results for benthic photograph analysis.

Bioturbation Level	# of photos	# of study sites
1 (very poor)	90 (7%)	2
2 (poor)	260 (21%)	6 (9*)
3 (moderate)	246 (20%)	8 (10*)
4 (heavy)	250 (20%)	10 (12*)
5 (very heavy)	391 (32%)	6 (8*)

* includes additional survey stations not used in statistical analysis due to incomplete data. Stations include WC5, S38, MT1, MT2, and four abyssal plain sites (JSSD1, JSSD2, JSSD4, JSSD5).

3.6.1. Very Poorly Bioturbated (Category 1)

Sediments meeting “very poorly bioturbated” criteria display featureless or near-featureless relief, lacking significant granulation visible to the naked eye. Animal tracks (if present) will often appear in pristine condition (Fig. 61).

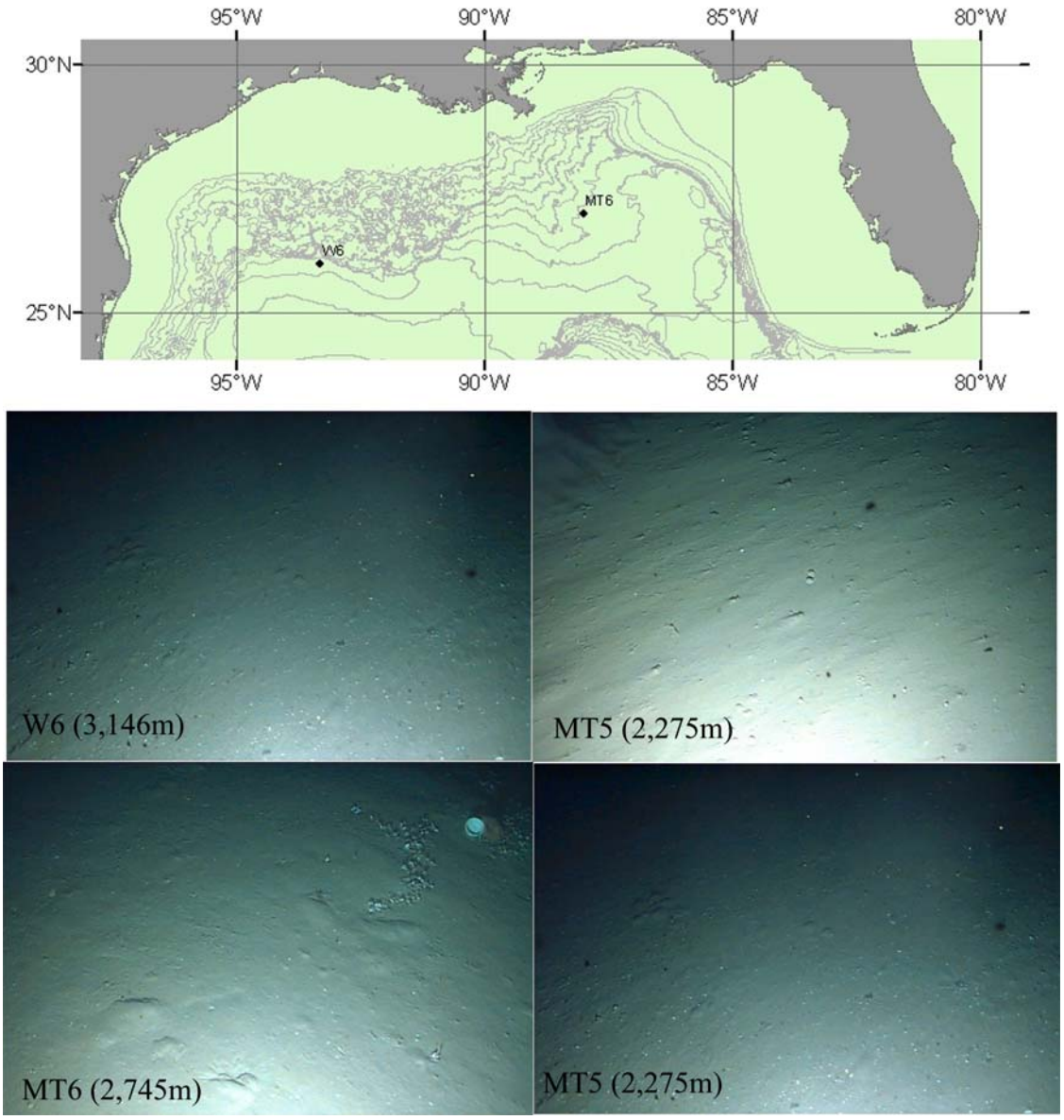

Fig. 61. Category 1 “very poor” bioturbation. Note human trash in right background of MT6 frame.

Only two survey stations were found to be “very poorly” bioturbated. These were both lower slope sites, widely separated from one another. Station MT6 is at the bottom of the Mississippi Canyon (2,745 m), and W6 (3,146 m) is in the western GoM. Both sites possessed low (< 2.4 uM) bottom-water POC values; station W6 measured the lowest POC (1.7 uM) in the study. Both category 1 stations measured low total macrofaunal abundances (< 1,900 m^2).

Mean polychaete, sedentary fauna, and motile crustacean abundances were also very low in comparison to mean values found at more highly bioturbated stations. For polychaete abundance, both category 1 sites ranked 3rd and 6th lowest overall (out of 32 total test stations). Station MT6 sampled 299 m^2, and W6 sampled 386 m^2. Sedentary fauna abundance for category 1 sites ranked 1st and 7th. The lowest value was for MT6 at the bottom of the Mississippi Canyon (2,745 m), with 95 m^2. W6 sampled 217 m^2. The average abundance between these two stations was less than half that seen for category 2-5 sites. A similar low abundance value was seen for mean motile crustacean abundance. Category 1 sites ranked 1st and 6th. Like that seen for sedentary fauna, station MT6 had the lowest motile crustacean abundance (227 m^2). W6 in the deep western GoM contained 369 m^2.

3.6.2. Poorly Bioturbated (Category 2)

Sediments meeting “poorly bioturbated” criteria show a minimal amount of sediment disturbance. Burrows are small and few in number, constituting less than 10% of surface area. Lacking the presence of visible mounds or burrows, coarse sediment granulation is abundant (Fig. 62).

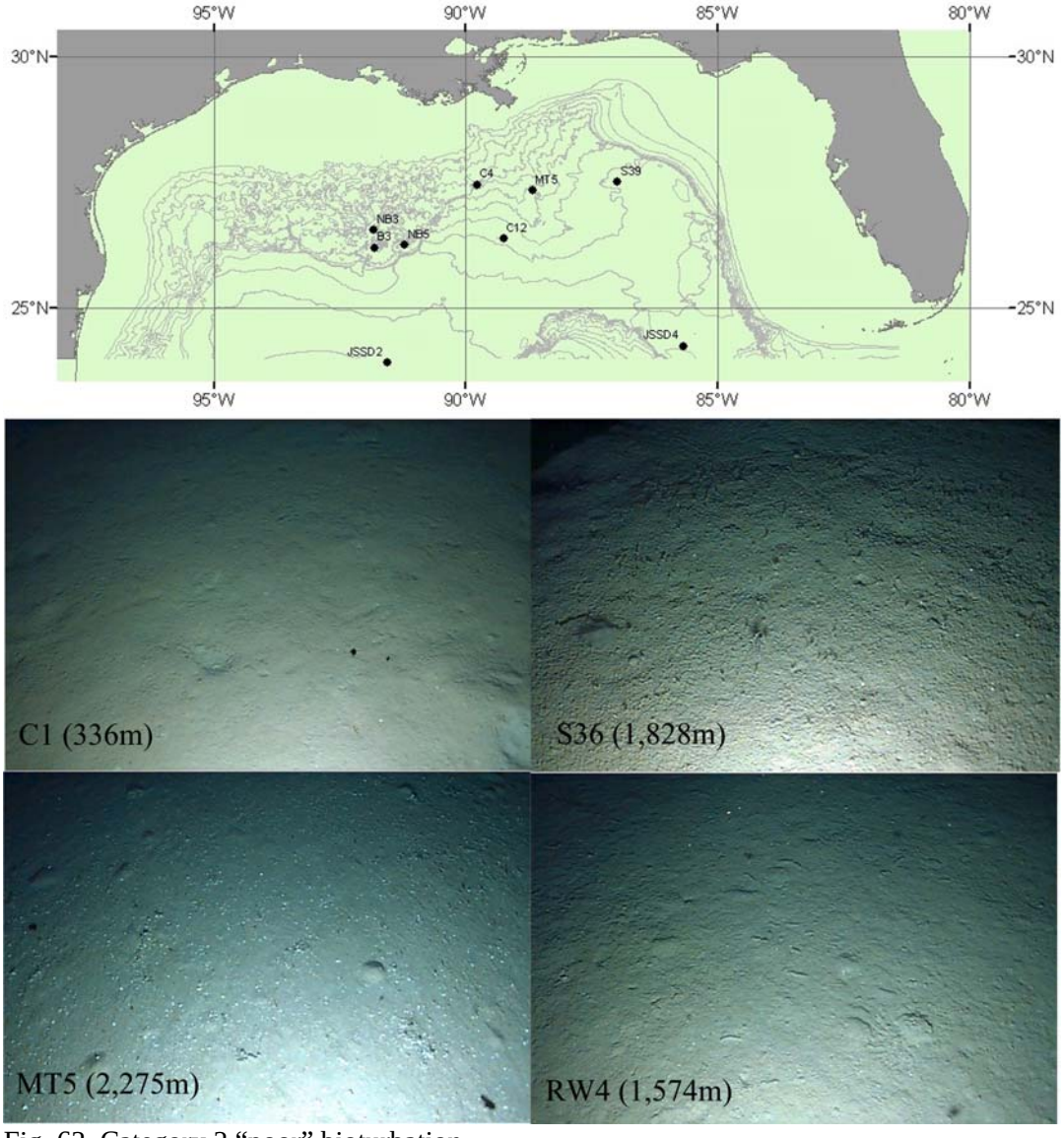

Fig. 62. Category 2 “poor” bioturbation.

Nine survey stations displayed “poor” bioturbation; six of these stations contained sufficient data for use in statistical testing. Category 2 stations tended to be relatively deep, ranging from 1,463 m (C4, north-central GoM) to 2,921 m (C12, central GoM). Most stations were found on the lower continental slope. In addition, two of the four photo-surveyed abyssal plain JSSD stations were also classified as category 2. Only one category 2 station (MT5) was located in a submarine canyon. In addition, only one category 2 station was located on the Florida Escarpment (S39), and at the bottom of it (2,997 m), at that.

Bottom-water POC values were higher than those of the two category 1 (very poorly bioturbated) stations, ranging from 2.5 uM (station C12 at 2,921 m in the central GoM) to 4.4 uM (C4 at 1,463 m, central GoM). Average POC between the six full data stations was 3.1 uM.

Total mean macrofaunal abundances for category 2 stations were in the lower 50-percentile (< 2,900 m^2), though there were two exceptions. Station C12 (2,921 m) sampled a relatively moderate total abundance (4,111 $m^{2)}$, and station C4 (1,463 m) a much higher value (6,687 m^2).

Mean polychaete abundance for category 2 stations was highly variable, ranging from the lowest two values (286-292 m^2) to the low end of the uppermost 30-percentile of stations (1,596 m^2). The average abundance between all six stations was 729 m^2, roughly equating to twice the polychaete abundance seen at category 1 sites, or less than half that seen at category 4 or 5 sites. The two lowest category 2 sites for polychaete abundance (B3, NB5) also happened to have the lowest values out of all bioturbation categories.

The category 2 station possessing the highest polychaete abundance (C4) was also the shallowest category 2 site (1,463 m). The next shallowest category 2 station was 400 m deeper (NB3, 1,875 m).

Mean sedentary abundance patterns for category 2 stations were similar to that seen for polychaetes, in that the shallowest station (C4) possessed the highest values (493 m^2). However, in regards to overall rankings against other DGoMB stations, sedentary faunal abundances at category 2 locations tended to favor the upper 50% on the ranking scale (although less than one-*seventh* the maximum sedentary abundance encountered). The average sedentary abundance for category 2 was 329 m^2.

Mean motile crustacean abundances were (again) highest (1,472 m^2) for the shallowest category 2 station (C4), as they were for polychaetes, sedentary fauna, and total macrofauna. Four of the six category 2 sites measured crustacean abundance values (408-562 m^2) in the second quartile range, but the remaining two sites (C12, C4) measured much higher values (1,164 and 1,472 m^2, respectively).

Category 2 bioturbation results are summarized in Table 14.

Table 14
Summary of category 2 bioturbation results.

"Poor" Bioturbation*:* 9 survey stations (6 used for statistics) *A.* lower continental slope and abyssal plain depths *B.* sediment POC values low (2.5 uM) to high (4.4 uM); averaging 3.1 uM *C.* mean macrofaunal abundances low (< 2,900 m^2)* *D.* mean polychaete abundances wide-ranging (286-1,596 m^2); average 729 m^2 E. mean sessile abundances relatively (first quartile) low (site NB5, 173 m^2) to third-quartile (279-494 m^2); average 329 m^2 F. mean motile crustacean abundances second quartile (408-562 m^2)**; average 776 m^2 * exceptions: station C12 (4,111 m^2) and C4 (6,687 m^2) ** exceptions: station C12 (1,164 m^2) and C4 (1,472 m^2)

3.6.3. Moderately Bioturbated (Category 3)

Sediments meeting “moderately bioturbated” criteria display burrow/mound presence taking up ~10-30% of sediment surface. No large megafaunal burrows or mounds are present. Some (centimeter-scale) vertical relief is present, but such relief does not dominate sampling fields (Fig. 63).

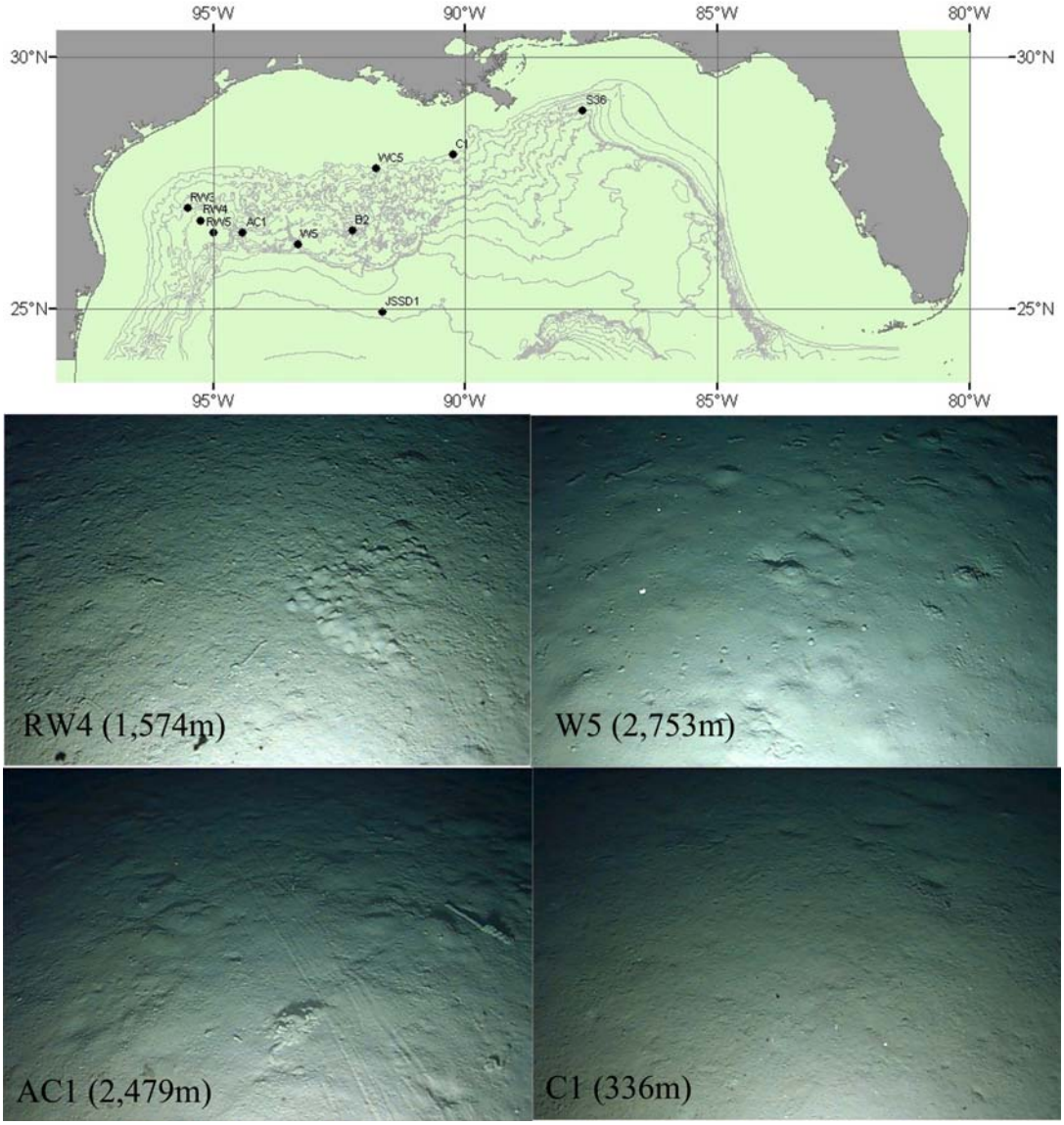

Fig. 63. Category 3 “moderate” bioturbation.

Ten survey stations displayed “moderate” bioturbation; eight of these stations contained sufficient data for use in statistical testing. Category 3 stations tended to be on average, slightly shallower (1,819 m) than category 2 stations (2,203 m). Most category 3 sites were encountered at mid-lower slope depths >1,300 m. Abyssal plain station JSSD1 (3,600 m) also met category 3 bioturbation criteria. Except for one station in the central GoM (C1, 336 m) and one in the northeast GoM (S36, 1,828 m), the remaining (seven) category 3 sites (including the abyssal plain station) were all found in the western GoM. Two stations were in submarine canyons; the deep Alaminos Canyon (AC1, 2,479 m), and the central DeSoto Canyon site (S36, 1,828 m).

The majority (6 of 8) of category 3 bioturbation stations possessed low (first quartile) bottom-water POC levels ranging from 1.9-2.5 uM. The lowest value was encountered in the deep Alaminos Canyon (AC1, 2,479 m). There were two category 3 stations with high POC values. Both of these were unusual from the other category 3 stations, but in different ways. Station S36 in the DeSoto Canyon (1,828 m) was the only category 3 site in the eastern GoM, and station C1 was by far the shallowest category 3 site (336 m). S36 had a POC content of 3.5 uM (upper third quartile), while C1 measured the second highest value for the entire study, 4.8 uM.

Total macrofaunal abundance for category 3 stations was generally on the low scale (< 3,100 m^2). Six of the eight full-data stations sampled abundances ranging from 1,585-3,057 m^2, averaging 2,287 m^2. The two exception stations were the same seen to possess atypically high bottom-water POC. The shallow water C1 station had a total mean abundance of 6,548 m^2 (upper end of third quartile), and S36 in the middle DeSoto

Canyon had 12,582 m^2. S36 measured the second highest macrofaunal abundance site in the study.

Mean polychaete abundance for category 3 was wide ranging across an *order of magnitude* difference, measuring between 324-3,589 m^2. Station S36 in the (middle) DeSoto Canyon measured the highest polychaete abundance (3,589 m^2) out of all DGoMB survey stations. Station C1, located on the central GoM shallow shelf/slope break (336 m), was the only other category 3 station with a high (fourth quartile) polychaete abundance (1,813 m^2). Five of the eight category 3 sites measured much lower (324-632 m^2) polychaete abundances and there was one site (RW3, far western GoM) measuring an intermediate abundance value (1,046 m^2). The two category 3 canyon sites measured almost completely opposing polychaete abundances. The deep Alaminos Canyon site (AC1, 2,479 m) had the fifth lowest polychaete abundance (347 m^2) out of all DGoMB sites, while the middle DeSoto Canyon site (S36, 1,828 m) was ranked 1st (3,589 m^2).

Category 3 sedentary fauna abundance patterns were roughly similar to those seen for polychaetes, although abundance values were more evenly distributed between the low (first and second quartile) ranges. The lowest sedentary abundance station was in the Alaminos Canyon (110 m^2); station AC1 was ranked 2nd lowest overall in sedentary abundance, only slightly ahead of the category 1 station MT6 (also in a very deep canyon). Two other lower continental slope, category 3 stations displayed similarly low sedentary fauna abundances; W5 in the deep western GoM (135 m^2), and the deep

western basin site B2 (137 m^2). These three were all found in water depths exceeding 2,000 m.

As noted for the polychaetes, high sedentary fauna abundances were seen for DeSoto Canyon station S36 and the very shallow shelf/slope break station in the central GoM (C1). However, in a reversal of the rank order of the two highest category 3 polychaete abundance sites, the higher value is at shallow C1 (2,300 m^2), while DeSoto Canyon station S36 measured 598 m^2. Station C1 ranked 3rd highest in sedentary abundance overall.

Like category 3 polychaete and sedentary fauna abundance values, those for motile crustaceans tended to skew towards the lower end of the scale (first and second quartiles, < 700 m^2). Six of the eight fully worked-up category 3 stations sampled motile crustacean abundances between 242 m^2 (W5, 2,753 m) and 629 m^2 (RW4, 1,574 m). Alaminos Canyon station AC1 had crustacean abundance values only slightly higher (290 m^2) than deep W5 (242 m^2), and W5 was ranked 2nd lowest overall. Similar to the pattern seen for sedentary fauna abundance, deep basin station B2 (310 m^2) joined AC1 and W5 as the three lowest crustacean abundance sites. These three sites were all located in the western GoM in water depths exceeding 2,000 m.

As seen for all other macrofaunal abundance measurements, DeSoto Canyon station S36 and shelf/slope station C1 continued to be the only two category 3 sites possessing upper scale (relative to other bioturbation categories) motile crustacean values. The middle DeSoto Canyon site S36 (1,828 m) had the highest abundance (2,014 m^2), and was ranked 4th highest overall. The central GoM shelf/slope station C1 (336 m)

measured a much lower crustacean abundance (904 m^2), though this still placed it in the upper 50-percentile ranking.

Category 3 bioturbation results are summarized in Table 15.

Table 15
Summary of category 3 bioturbation results.

"Moderate" Bioturbation*:* 10 survey stations; 8 used for statistics *A.* various water depths from shelf/slope break to abyssal plain; generally middle-lower continental slope (>1,300 m) *B.* sediment POC values usually* very low (first quartile), averaging 2.3 uM *C.* mean macrofaunal abundance usually* low (first and second quartiles; < 3,100 m^2) *D.* mean polychaete abundances wide ranging between low (site B2, 324 m^2) to very high (site S36, 3,589 m^2), with majority of values in lower 30-percentile. Average 1,204 m^2 *E*. mean sessile abundances wide ranging between very low (site AC1, 110 m^2) to very high (site C1, 2,300 m^2), with majority of values in lower 50-percentile. Average 517 m^2 F. mean motile crustacean abundances usually* on low end of scale (242-630 m^2), with majority of values in lower 50-percentile. Average (excluding high outliers) 474 m^2 (667 m^2 including outliers*) * exceptions: stations C1, S36 (much higher values where indicated)

3.6.4. Highly Bioturbated (Category 4)

Sediments meeting “highly bioturbated” criteria are characterized by 30-60% of surface area disturbed by mound/burrow features. Some burrow/mounds are large, overlapping smaller ones. Dominant vertical relief is at small (centimer) scales (Fig. 64).

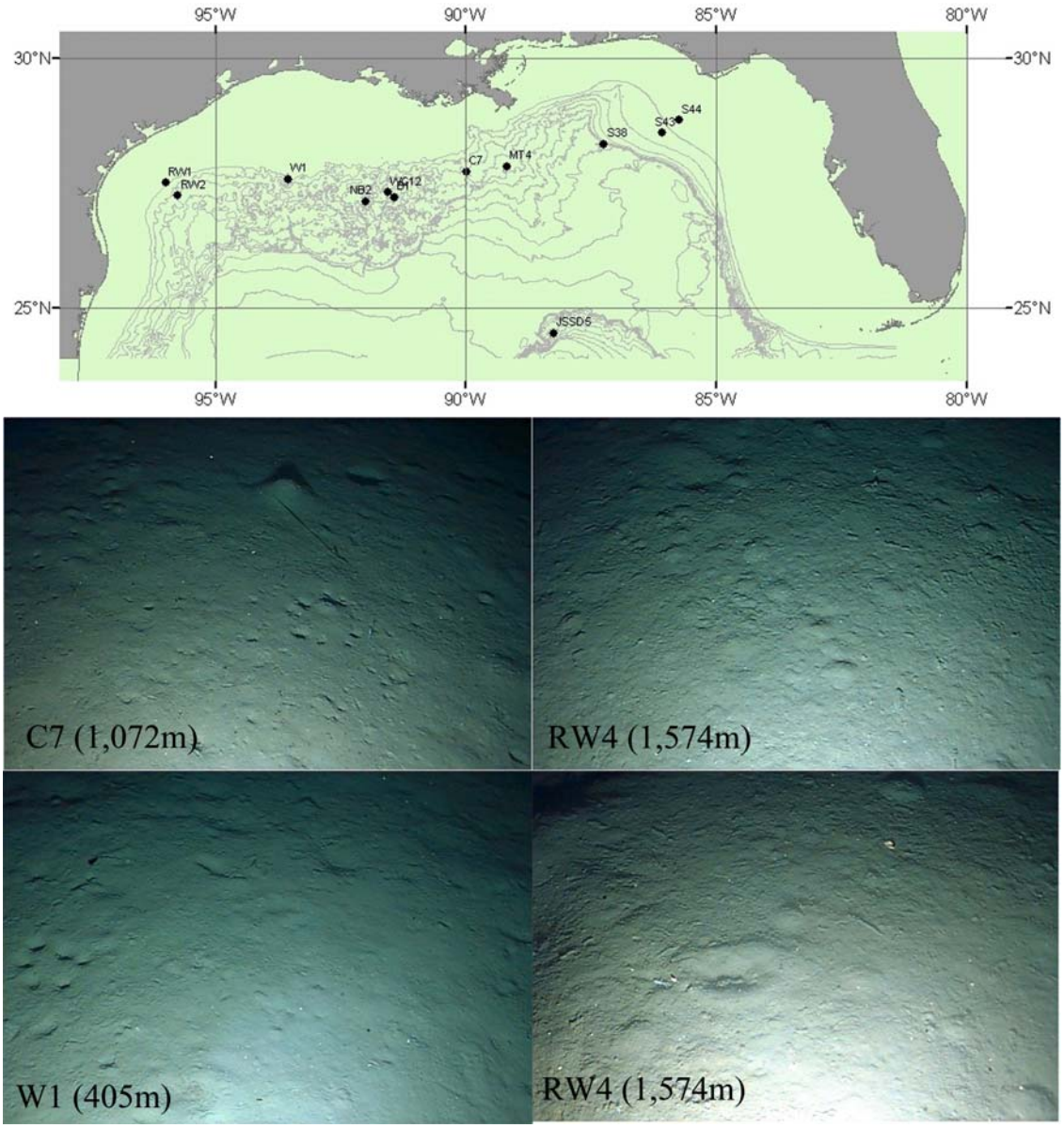

Fig. 64. Category 4 “high” bioturbation.

"Highly" bioturbated sites were evenly dispersed throughout the northern GoM, generally located at shelf/slope transitional and upper slope depths. Only one location (MT4; 1,401 m) was within a submarine canyon. Three sites were located on the Florida Escarpment, two of which were at shelf/slope depths < 400 m, and the third on the lower slope (S38; 2,600 m). One of the JSSD abyssal plain stations (JSSD5; 3,350 m) also met category 4 criteria.

Twelve survey stations displayed high bioturbation; ten of these stations contained sufficient data for use in statistical testing. This was the most commonly encountered seafloor bioturbation category.

Category 4 stations measured bottom-water POC values that were generally higher (evenly split between second, third, and fourth-quartile rankings) than category 3 stations (mostly first quartile), ranging from 2.6 uM (MT4, middle Mississippi Canyon) to 4.7 uM (S44, shallow Florida escarpment). The average category 4 POC value was 3.5 uM. The three category 4 stations possessing the highest POC content (> 4.1 uM) were all located in very shallow (< 500 m) water.

Total mean macrofaunal abundance all ranked between the upper second quartile to the mid-fourth quartile. Values ranged from a low of 3,358 m^2 (NB2, central GoM at 1,530 m) to a high of 9,393 m^2 (RW1 in far western GoM, 213 m). The average category 4 macrofaunal abundance value was 6,218 m^2. Six of the 10 full-data survey stations measured high abundances > 6,000 m^2. Four of these six (constituting all category 4 shelf/slope areas) possessed total abundances >6,800 m^2.

Mean polychaete abundance for category 4 stations showed a similar rank pattern to that of total mean macrofaunal abundance (all values in upper 60-percentile). All category 4 polychaete abundance measurements exceeded 700m^2. The lowest abundance (785 m^2) was seen at deep basin site B1 (2,255 m). This was the only category 4, lower continental slope site that could be measured for mean polychaete abundance. However, the next two lower-ranked abundance stations were also deeper relative to other category 4 sites. These were NB2 (1,530 m) and WC12 (1,166 m), sampling polychaete abundances of 915 m^2 and 933 m^2, respectively.

The highest polychaete abundance (3,264 m^2) was measured at shallow shelf/slope station S44 (213 m) on the Florida Escarpment. This was the second highest value encountered for polychaete abundance overall (category 3 station S36 had 3,589 m^2). As observed for total macrofaunal abundance, category 4 sites with higher polychaete abundances tended to be among the shallow shelf/slope sites, with lower polychaete abundances encountered on the continental slope proper.

Sedentary fauna abundances at category 4 stations were wide ranging over an order of magnitude, with values 219-2,779 m^2, averaging 1,105 m^2. As seen for total macrofauna and polychaete abundances, sedentary abundances were highest at the shelf/slope transitional zone depths. All four category 4, shelf/slope sites had sedentary fauna abundances greater than 1,500 m^2. Out of all bioturbation study sites, the category 4 stations RW1 (2,654 m^2) and W1 (2,779 m^2) had the highest sedentary fauna abundances. *Non*-shelf/slope category 4 stations possessed significantly lower sedentary macrofaunal abundance. All six of these upper and lower continental slope stations

sampled less than 430 m2, and averaged 299 m^2. The lowest-ranked category 4 station was WC12 (1,166 m; 219 m^2) in the west-central GoM.

Motile crustacean abundances for category 4 sites exceeded (with one exception) 600 m^2, peaking as high as 2,308 m^2. The average value was 967 m^2. Compared to other DGoMB bioturbation study sites, category 4 crustacean abundances were ranked (with one exception) in the upper 60-percentile. Unlike the patterns seen for other macrofaunal abundance factors, motile crustacean abundances for category 4 stations were not skewed towards shallow shelf/slope depths. Motile crustaceans did not appear to favor *any* particular depth range between the ten category 4 bioturbation sites. The two category 4 stations with the highest motile crustacean abundances were C7 in the central GoM (2,308 m^2, ranking 3rd highest overall), and MT4 in the mid-slope Mississippi Canyon (1,236 m^2, ranking 7th overall). Shelf/slope station S44 (213 m) on the Florida Escarpment was the only category 4 station measuring a relatively low (359 m^2) motile crustacean abundance.

Category 4 bioturbation results are summarized in Table 16.

Table 16
Summary of category 4 bioturbation results.

"High" Bioturbation*:* 12 survey stations; 10 used for statistics *A.* Usually* shallower depths (213-1,530 m), shelf/slope zone and upper slope *B.* sediment POC all ranked upper 75-percentile. Values 2.6-4.7 um; average 3.5 uM *C.* mean macrofaunal abundances all upper 60-percentile (3,358-9,393 m^2); average 6,218 m^2 *D.* mean polychaete abundances all upper 60-percentile (785-3,264 m^2); average 1,725 m^2 *E*. mean sessile abundances all upper 75-percentile (219-2,779 m^2); average 1,105 m^2 *F*. mean motile crustacean usually** all upper 60-percentile (> 600 m^2); maximum value 2,311 m^2; average (including outlier**) 967 m^2, without outlier 1,038 m^2 * exceptions: lower slope and abyssal plain stations S38, B1, JSSD5 ** exception: station S44 (359 m^2)

Sediments meeting “very highly bioturbated” criteria show over 75% of the visual field distinctly stirred up with mounds/burrows. Evidence of large sediment excavations by large megafauna (i.e. *Chaceon*, *Bathynomus*) is visible. Examples of category 5 images are shown in fig. 65.

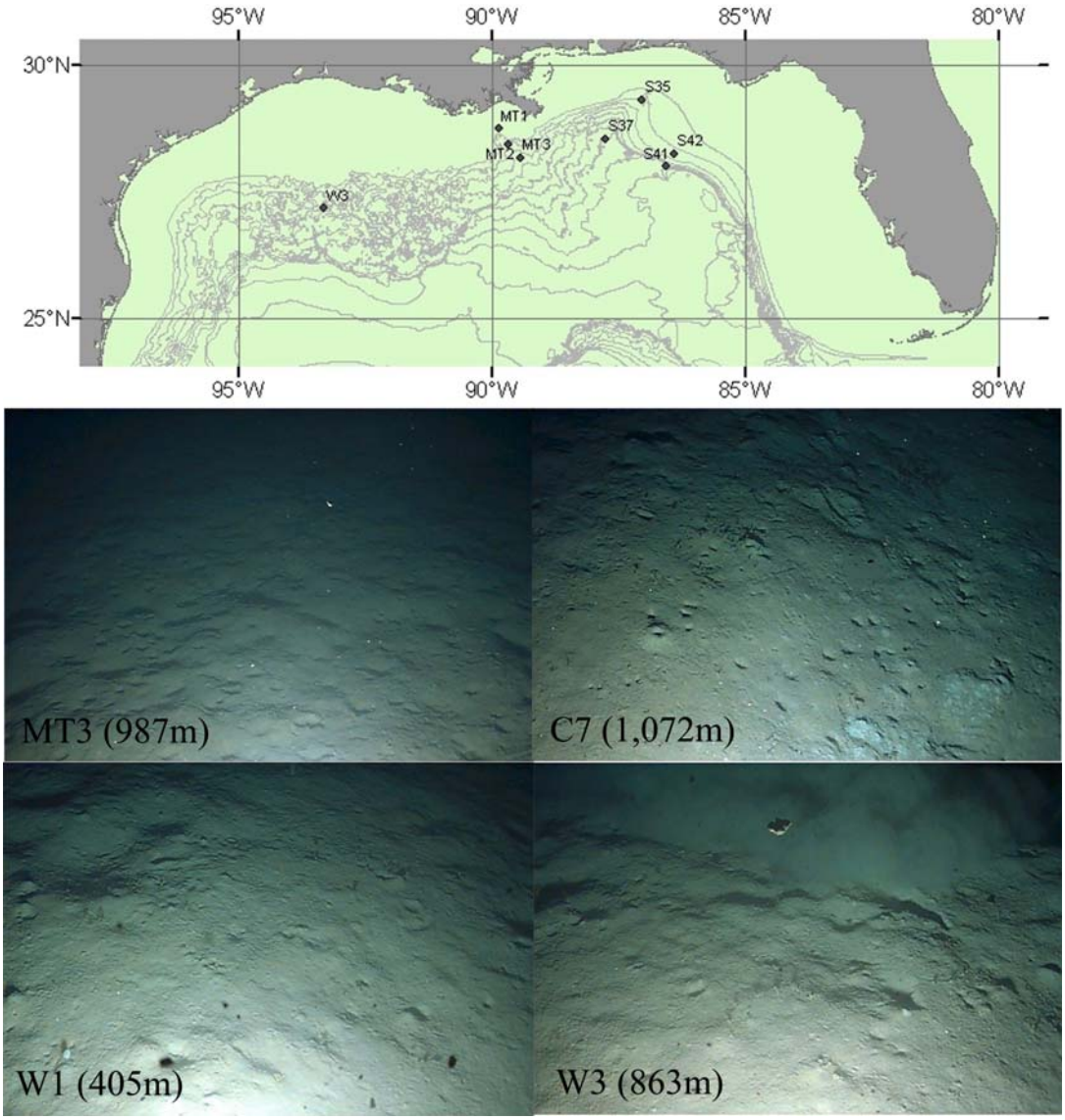

Fig. 65. Category 5 “very heavy” bioturbation.

Eight survey stations displayed “very high” bioturbation; six of these stations contained sufficient data for use in statistical testing (upper-Mississippi Canyon stations MT1 and MT2 were the two exception sites). Seven of the eight sites were located in the eastern GoM. The exception was W3 (863 m) in the western GoM. Other than two lower continental slope stations (S37, S41), the remainder of stations exhibiting category 5 bioturbation were found on the upper slope less than 1,000 m deep. Five (out of eight) stations were located in submarine canyons; specifically all three upper Mississippi Canyon sites, and the shallow and deep DeSoto Canyon sites.

As a group, bottom-water POC values for category 5 stations were higher than for other bioturbation categories. Five of the six stations ranked in the upper 50-percentile (3.2-7.3 uM). The single low-POC site (2.3 uM) was located on the deep Florida Escarpment (station S41, 2,979 m). Four out of five of these higher-POC stations fell within a narrow depth zone (663-987 m) in which large, common megafaunal burrowers like the isopod *Bathynomus giganteus* or the brachyuran *Chaceon quinqedens* are known to be commonly encountered (Pequegnat, 1983).

The DGoMB station possessing the highest bottom-water POC content (7.3 uM) was the shallow DeSoto Canyon site (S35). Station S35 also sampled the third highest macrofaunal abundance value overall (10,972 m^2).

Total mean abundance values were (on average) 11% higher than those seen at category 4 sites, ranging from a low of 3,800 m^2 at the deep Florida Escarpment station S41 (which also had the lowest category 5 POC), up to as much as 14,004 m^2 in the mid-slope Mississippi Canyon (MT3). The second (10,972 m^2) and third highest (6,318 m^2)

category 5 macrofaunal abundance sites were also within submarine canyons (S35 and S37 in the DeSoto Canyon).

Mean polychaete abundance for category 5 stations averaged 1,668 m^2, but values ranged widely between 579-2,982 m^2. The two highest abundance stations (MT3, S35) were both located within submarine canyons at upper continental slope depths. MT3 (987 m) in the Mississippi Canyon was ranked 3rd highest out of DGoMB survey stations, with a mean polychaete abundance of 2,981 m^2. S35 (663 m) in the DeSoto Canyon was ranked 4th overall, with essentially the same mean abundance (2,970 m^2). There was one other category 5 station located in a submarine canyon, but it was at a much deeper depth. Station S37 (2,384 m) in the lower DeSoto Canyon sampled 1,311 m^2, ranking it in the upper third quartile.

The deepest category 5 station (S41) measured the lowest polychaete abundance. Station S41, located near the bottom of the Florida Escarpment, had an abundance of 579 m^2. This was still twice the abundance value seen for nearly half of the category 1 and 2 stations found at similar lower slope depths.

The single category 5 station encountered in the western GoM (W3, 863 m) measured a polychaete abundance of 840 m^2 (ranked upper 2nd quartile). Station W3 also had the distinction of being the *upper* slope DGoMB station with the lowest overall polychaete abundance.

Mean sedentary fauna abundance for category 5 sites ranged from 181-683 m^2, averaging 365 m^2. Values were wide-ranging between all quartile ranks, with survey stations evenly split between upper and lower 50-percentile rankings. Very high

sedentary abundance values (>1,500 m^2) seen for some of the category 3 and 4 stations were not encountered at any category 5 stations. As determined for polychaetes and total macrofauna, the highest (value) category 5 station was the Mississippi Canyon site MT3 (683 m^2, ranked 6th overall). However, unlike polychaete and total macrofauna, the next highest sedentary abundance site was tied between the upper DeSoto Canyon site S35 (402 m^2) and the non-canyon, upper Florida Escarpment site S42 (403 m^2).

Deep Florida Escarpment station S41 had the lowest category 5 sedentary abundance (181 m^2), as it also did for total macrofauna and polychaetes. The only other lower slope category 5 station (S37, lower DeSoto Canyon, 2,384 m) sampled an abundance of 290 m^2. The single western GoM category 5 site (W3) had a sedentary abundance (229 m^2) intermediate between the two deep slope stations, but was much shallower in depth (863 m).

Mean motile crustacean abundances were highest at category 5 stations. Averaging 1,754 m^2, the highest category 5 abundances (and the highest out of all DGoMB stations) were seen at the two upper-slope canyon sites. Station MT3 (987 m) measured 4,003 m^2, and S35 (663 m) had 2,502 m^2. The deep DeSoto Canyon station (S37, 2,384 m) sampled the next highest (ranked 6^{th} overall) crustacean abundance (1,434 m^2). The category 5 site with the lowest crustacean abundance (470 m^2) was deep escarpment station S41 (2,979 m), which was only half the abundance seen at the next lowest (963 m^2) category 5 site, station W3 in the western GoM.

Category 5 bioturbation results are summarized in Table 17.

Table 17
Summary of category 5 bioturbation results.

"Very High" Bioturbation: 8 survey stations; 6 used for statistics
A. mostly upper continental slope depths < 1,000 m
B. sediment POC values mostly* upper 50-percentile (3.2-7.3 uM)*; average 4.0 uM
C. mean total macrofaunal abundances mostly* upper 60-percentile (3,800-14,004 m^2)*; average 7,008 m^2
D. mean polychaete abundances mostly* upper 60-percentile (841-2,982 m^2)*; average 1,668 m^2
E. mean sessile abundances wide-ranging (181-683 m^2) between all quartile rankings; average 365 m^2
F. mean motile crustacean mostly* upper 40-percentile (963-4,003 m^2)*; average 1,754 m^2
*exception: station S41 (2.3 uM POC, 2,200 m^2 total macrofauna, 579 m^2 polychaetes, 470 m^2 motile crustaceans)

3.7. Factors Related to Seafloor Bioturbation

Sample data from 32 DGoMB survey stations was placed into a non-parametric correlation matrix (Kendall's *tau*-b) to look for factor associations with bioturbation. Factors having correlations greater than 0.25 (statistically significant at the 0.05 level) were entered into univariate and multivariate regressional analyses to look for factor relationships. Linear regressional relationships with bioturbation possessing r^2 values greater than 0.20 are shown in Table 18.

Table 18
Significant linear regressional relationships to megafaunal bioturbation.

Test Variable	linear r^2
Water Depth	-0.28
POC	0.20*
Total Mean Abundance	0.32*
Mean Polychaete Abundance	0.25*
Mean Motile Crustacean Abundance	0.21*

* Independent variable LOG_{10}-transformed

Averages values (ordered by bioturbation ranking) of test factors from Table 18 are summarized in Table 19.

Table 19
Summary of dominant averages of statistically significant bioturbation test variables. DGoMB stations lacking complete data sets (i.e. JSSD stations, MT1, MT2) are omitted.
* values excluding atypical outlier values.

Surface Bioturbation	Very Low (1). n=2	Low (2). n=6	Moderate (3). n=8	High (4). n=10	Very High (5). n=6
Water Depth (m)	2,946	2,203	1,819 (2,030*)	957	1,440 (820*)
Bottom-water POC (uM)	2.1	3.1	2.7 (2.3*)	3.5	3.3
Total Mean Abund. (#/m^2)	1,673	3,256	4,107 (2,287*)	6,218	7,004
Mean Polychaete Abund.	342	729	1,204	1,828	1,668
Mean Sedent. Abund.	156	329	517	1,105	365
Mean Motile Crust. Abund.	298	776	667 (474*)	967 (1,034*)	1,754 (2,010*)

3.7.1 Water Depth in Relation to Bioturbation Intensity

As a general rule, seafloor bottom along the shelf/slope break and upper continental slope tended to be more heavily bioturbated than sediments on the lower continental slope (Fig. 66). The majority of category 4 and 5 bioturbation stations were measured at depths shallower than 1,500 m. Of the ten survey stations shallower than 1,000 m, all but one (C1, category 3) was determined to be a category 4 or 5. The two shallowest stations (RW1, S44) were both sampled at 213 m, and fell under category 4 criteria. Category 5 ("very heavily bioturbated") conditions were first encountered at 663 m. Most category 5 stations were seen in water shallower than 1,000 m.

At deeper slope depths, bioturbation patterns were less distinct. Excepting one station (C4; 1,463 m), all category 1 and 2 sites were found in waters deeper than 1,800 m. The only two sites that met category 1 ("very poorly bioturbated") were both sited near the

bottom of the continental slope. Almost half of the “moderately bioturbated” (category 3) stations were also encountered at lower slope depths, as were two category 5 stations (S37, S41).

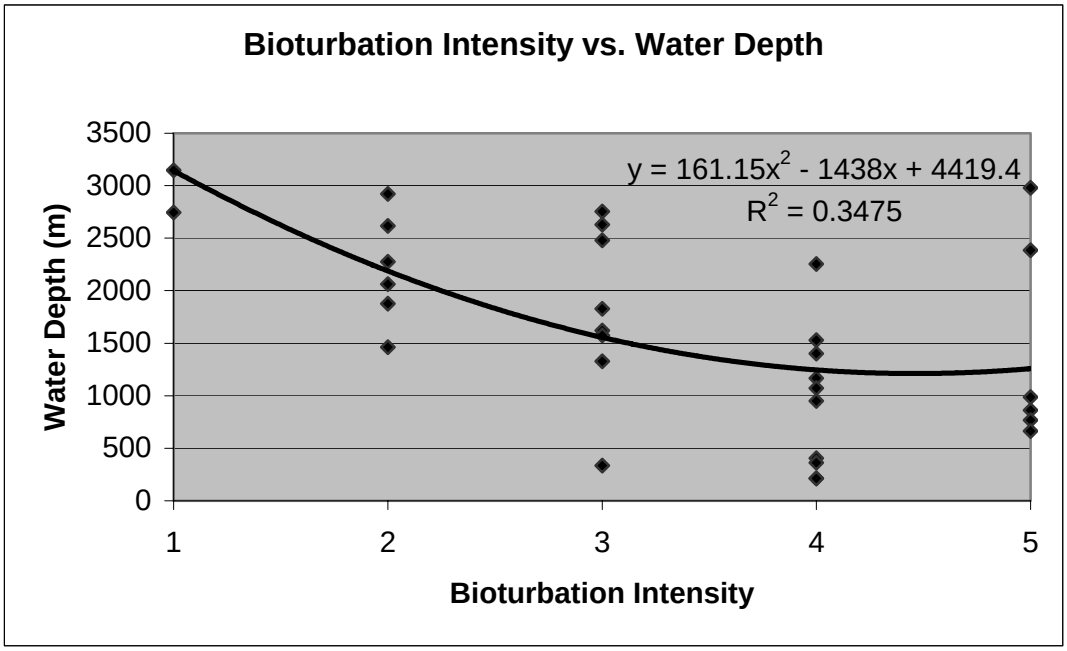

Fig. 66. Bioturbation intensity in relation to water depth. Regressional model used is second-order polynomial.

3.7.2. Bottom-water POC in Relation to Bioturbation Intensity

Although less discrete than that seen for water depth, there was a weak positive relationship between bottom-water POC content and bioturbation intensity. This is illustrated in Fig. 67.

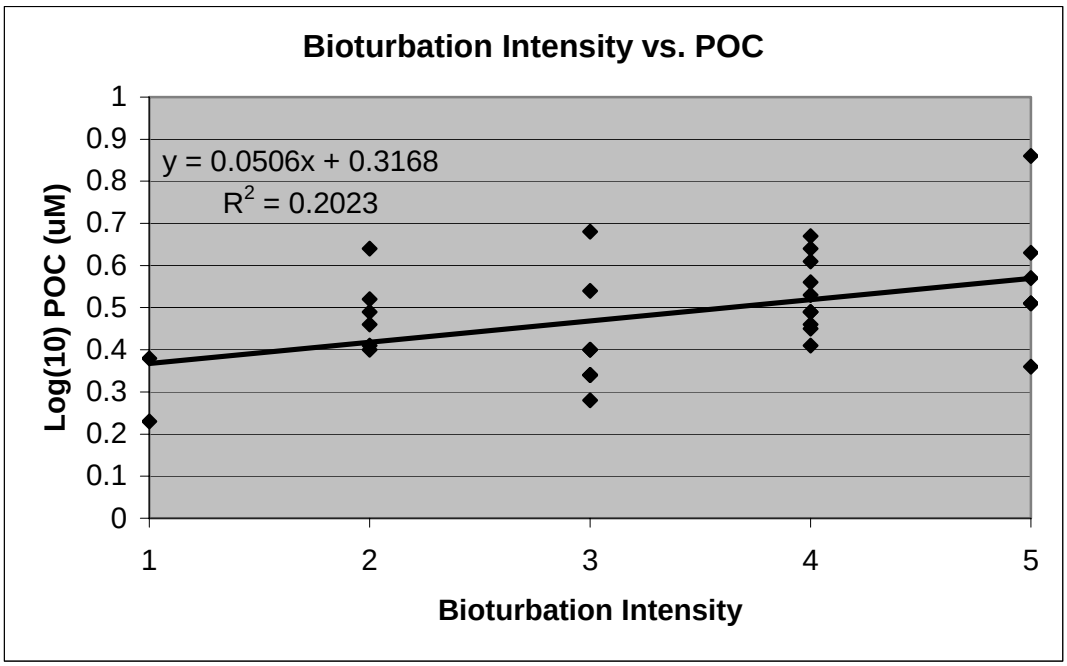

Fig. 67. Bioturbation intensity in relation to bottom-water POC content. POC values are LOG_{10}-transformed. Regressional model used is linear.

3.7.3. Faunal Abundances in Relation to Bioturbation Intensity

There was a weak positive relationship between bioturbation intensity and total mean macrofaunal, polychaete, and motile crustacean abundances. These are illustrated in Figs. 68, 69 and 70.

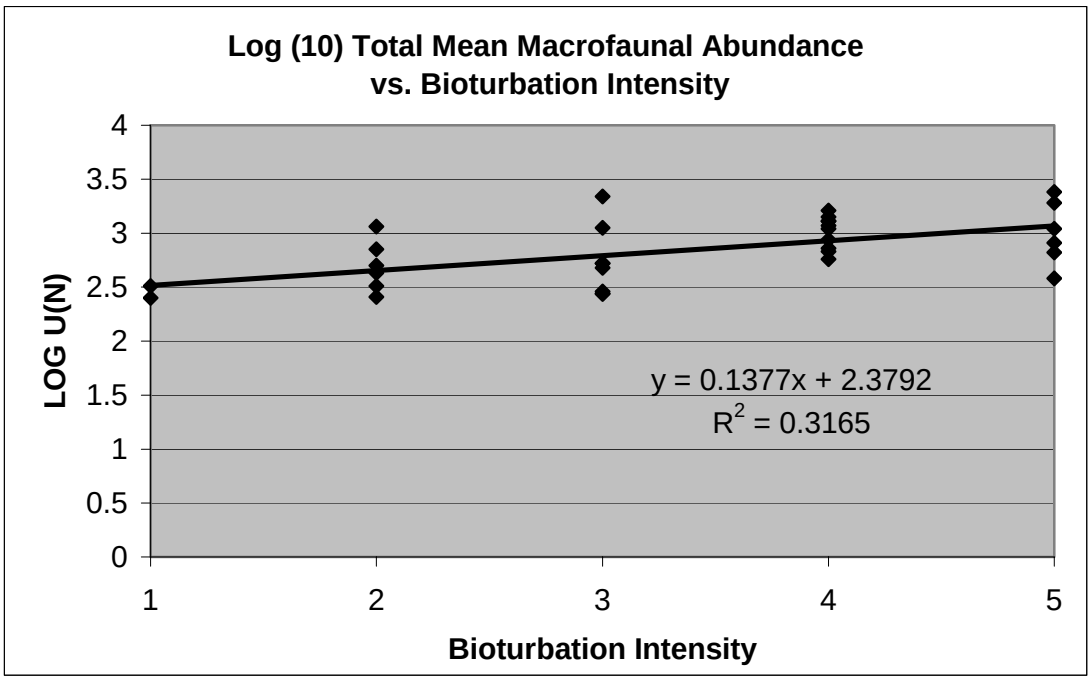

Fig. 68. Bioturbation intensity in relation to total mean macrofaunal abundance. Abundance values are LOG_{10}-transformed. Regressional model used is linear.

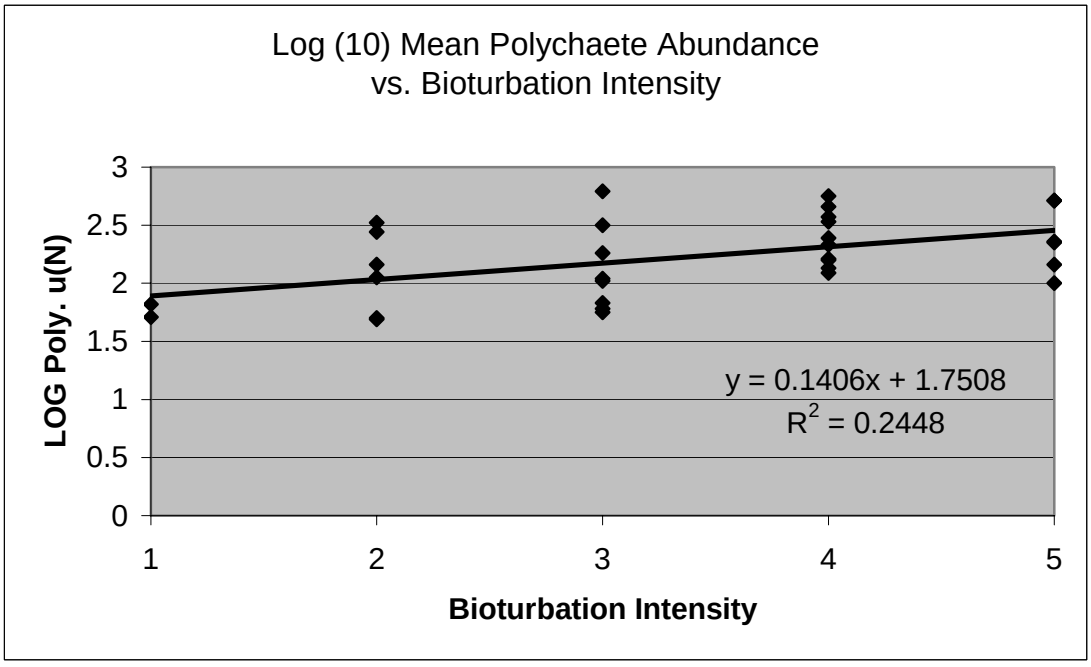

Fig. 69. Bioturbation intensity in relation to mean polychaete abundance. Abundance values are LOG_{10}-transformed. Regressional model used is linear.

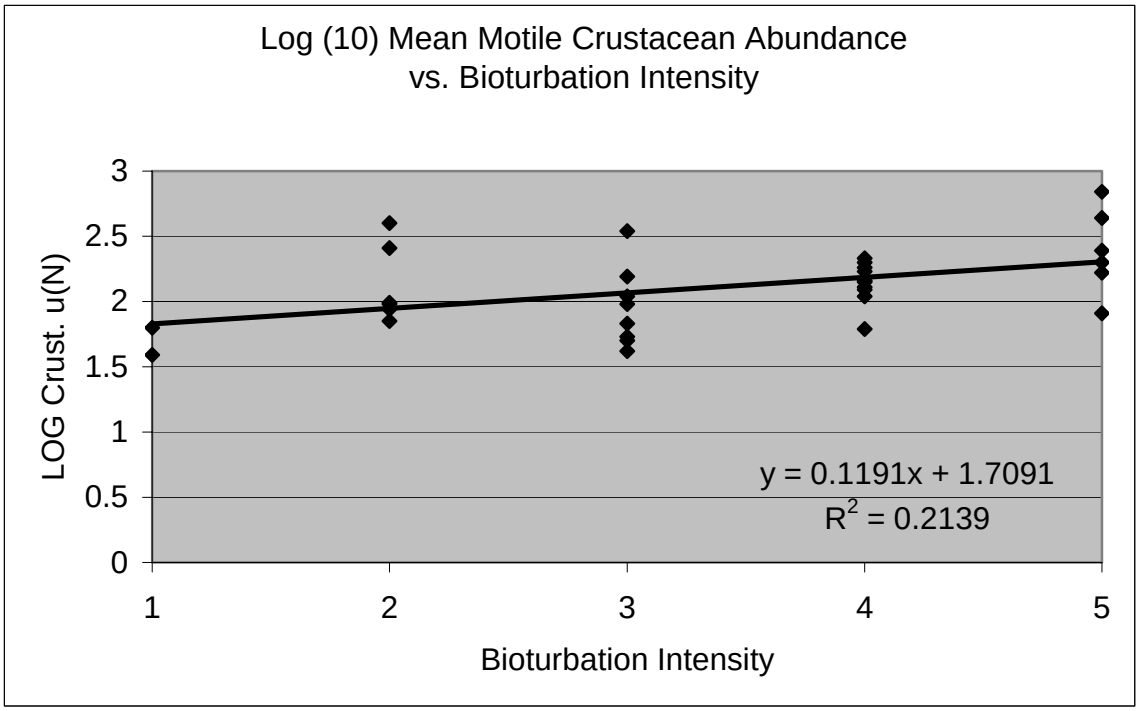

Fig. 70. Bioturbation intensity in relation to mean motile crustacean abundance. Abundance values are LOG_{10}-transformed. Regressional model used is linear.

3.8 Comparison of Two Different Bioturbation Photographic Techniques

As noted in Methods, the author's bioturbation measurements were directly compared against another system used by Ziegler (2002). Sediment bioturbation was evaluated using a similar protocol (Table 20) to the one used in this study, using the same photographs. DGoMB bottom images were visually evaluated on the basis of percent surface coverage by lebensspuren, specifically "tubes, tracks, and burrows".

Table 20
Criteria used to measure bioturbation by Ziegler (2002).

Bioturbation Level	% Lebensspuren
Low	<10
Medium	10-50
High	>50

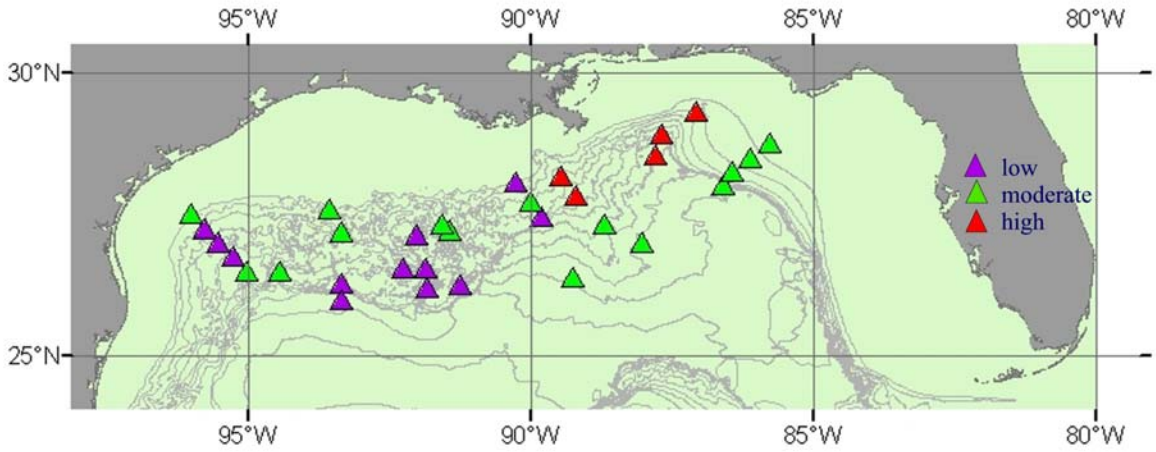

Fig. 71. Benthic bioturbation rankings using values from Ziegler (2002).

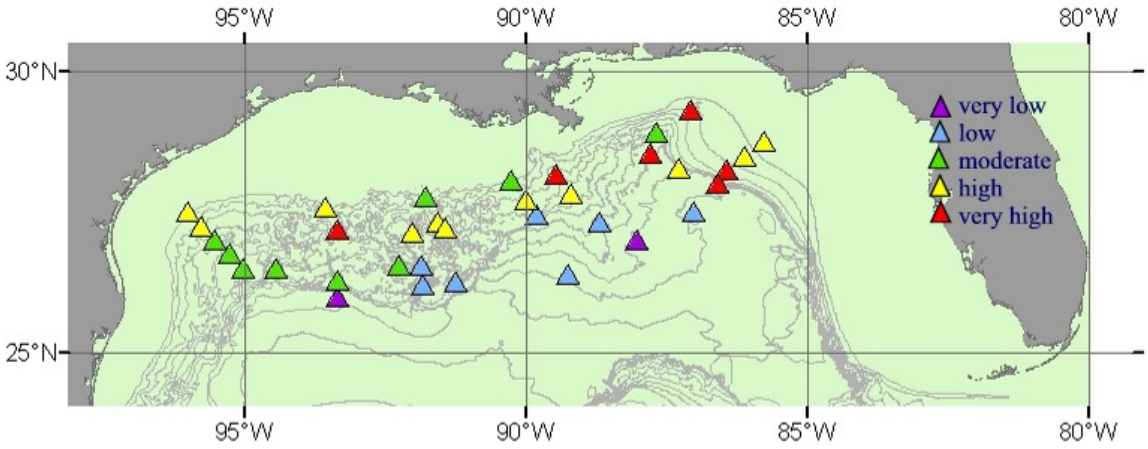

Fig. 72. Basin-wide map showing benthic bioturbation rankings at DGoMB survey sites, using criteria from Fig. 7.

Table 21
Basin-scale comparisons of bioturbation values between present study and that from Ziegler (2002). "Moderate" ranking from Ziegler study overlaps "moderate" and "high" values from author's study.

Physiographic Regions	Bioturbation (This Study)	Bioturbation (Ziegler , 2002)
Eastern GoM	high	moderate-high
Western GoM	moderate-high	low-high
Upper canyons:	high	high
Lower canyons	low-moderate	moderate-high
Escarpment	high	moderate-high
Very deep sites	low	low-moderate

Comparisons between the bioturbation values from both Ziegler's study (Fig. 71) and ours (Fig. 72) showed considerable differences in many cases (Table 21). It is likely that the criteria used for determining "lebensspuren" were at least partially to blame for this. Whereas our study focused on mounds and burrows only as lebensspuren indicators, the Ziegler study included other types (tracks, trails) of animal traces. Our study also placed some reliance on sediment stippling and local relief, which the Ziegler study would have omitted if such features could not be identified as lebensspuren.

3.9. Near-bottom Particulate Organic Carbon (POC)

Bottom-water POC content ranged from 1.7-7.3 uM, averaging 3.2 uM among the 32 DGoMB study sites examined. As expected (for surface-derived organic matter), POC generally declined in relation to water depth, with all twelve low-POC stations (< 2.6 uM) no shallower than 1,000 m and usually much deeper (Fig. 73). POC levels were also typically greater in the eastern GoM (Fig. 74).

POC was very strongly correlated to all macrofaunal abundances (Figs. 15, 22, 31, 45), indicating that it was a useful trophic measurement. For use in local-scale macrofaunal community analysis, POC was negatively correlated to taxonomic patchiness of total macrofauna and abundance patchiness of motile crustaceans (Fig. 60).

High (>60%) motile crustacean abundance patchiness only was seen where near-bottom POC was *less* than 3 uM. Local-scale abundance patchiness values for polychaetes and sedentary fauna did not exhibit this relationship to POC as did the motile crustaceans, suggesting that the former groups' local-scale dispersal patterns are more generalized or better cued to some other factor. The greater mobility of the motile crustaceans, combined with their high ratio of scavengers, carnivores, and selective particle feeders (Gage and Tyler, 1991; Cartes and Sorbet, 1996), likely allow these organisms to exploit local-scale habitats very effectively. At POC levels greater than 3 uM, motile crustacean abundances in some areas can exceed 2,000 m^2, but below 3 uM they fell below 1,400 m^2. Bottom-water POC at 3 uM may act as a trophic barrier of sorts for motile crustaceans, which when exceeded, facilitates greater dispersal (but not corresponding levels of *aggregation*) locally, and possibly exhibit abundance peaks. Although ecological patterns of macrofaunal crustaceans are very poorly known, examination of food supply-linked reproductive activity in studied species of cumaceans (Cartes and Sorbet, 1996), isopods (Kaim-Malka, 1998), and amphipods (Blankenship et al., 2006) may account for some of this low abundance patchiness via widespread release of young into the community.

The negative relationship to POC and local-scale dissimilarity of taxa (Fig. 57) is also likely an example of a trophic barrier to local fauna dispersion. With reduced macrofaunal abundance at low-POC sites, the many macrofaunal taxa that are normally not very common (i.e. aplacophorans, gastropods, priapulids) become even rarer, resulting in a more patchy local distribution of taxa. This assertion is further supported by examination of mean taxonomic richness (Fig. 75), which showed declines correspondingly to the (lower values) of POC.

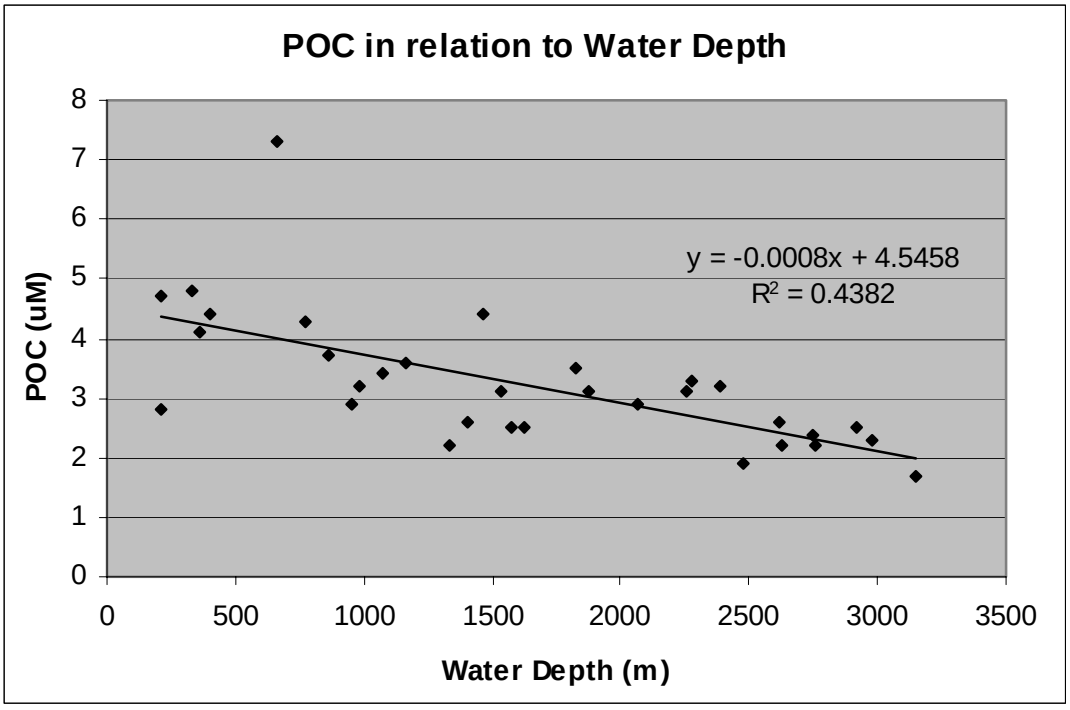

Fig. 73. Bottom-water POC in relation to water depth. Regressional model used is linear.

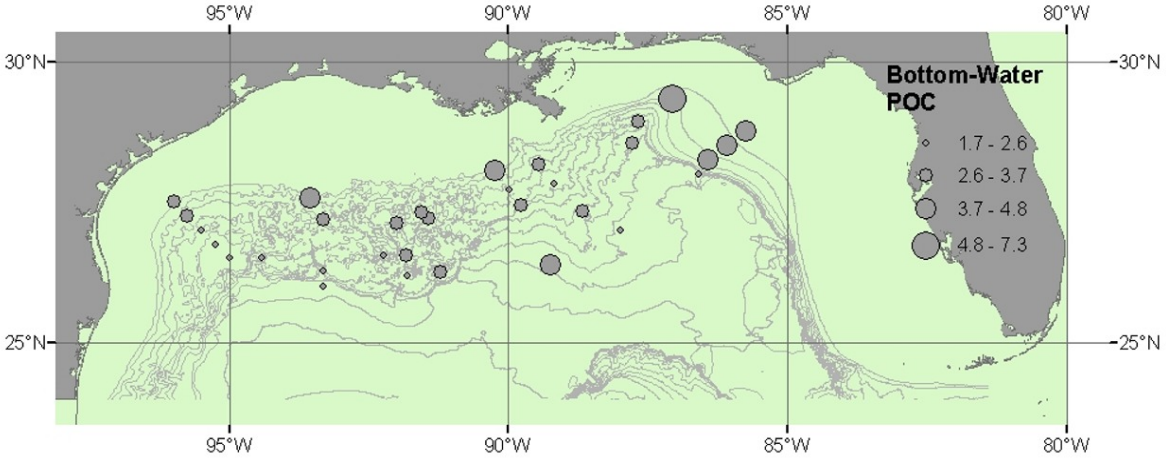

Fig. 74. Bottom-water POC values for the northern Gulf of Mexico. Units are expressed in uM.

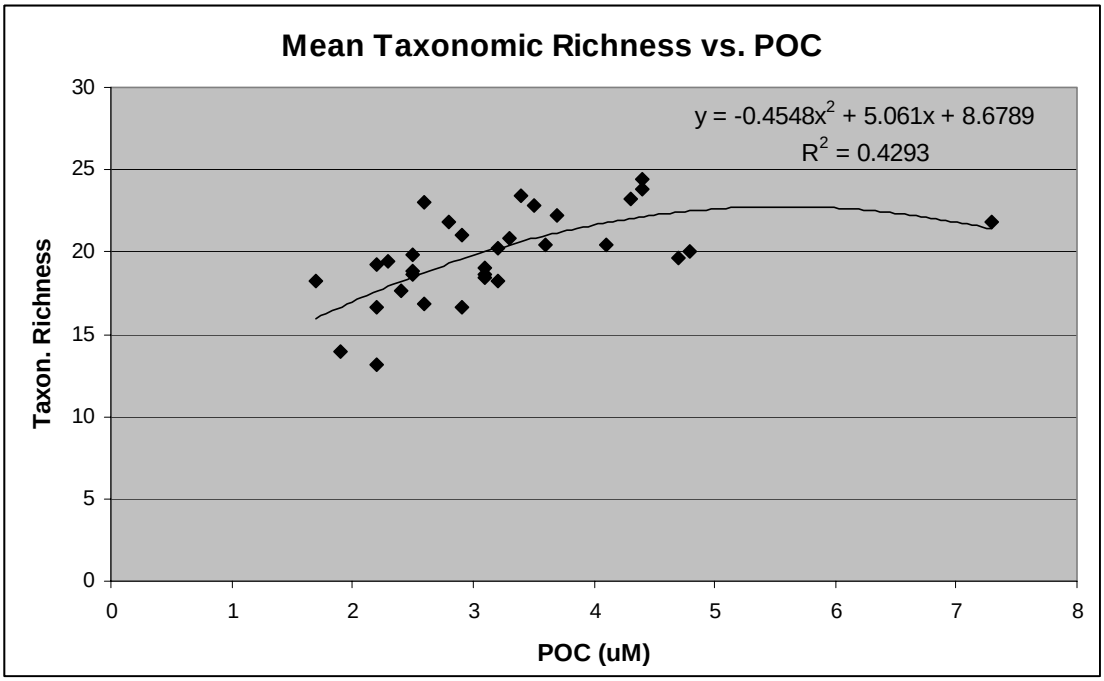

Fig. 75. Mean taxonomic richness in relation to near-bottom POC. Regression model used is second-order polynomial. The pattern of the curve indicates that lower POC restricts the number of macrofaunal taxa, but at higher levels (> 3uM), the effect begins to plateau, and may even create a negative feedback at higher levels (although there are too few high-POC data points to strongly support this).

3.10. Sediment Total Organic Carbon (TOC)

Sediment total organic carbon ranged from 0.03-1.98%, averaging 0.76% between the 31 survey stations examined. The majority (68%) of values fell within half a percent of one another (0.5-1.0% TOC). Gulf-wide patterns are shown in Fig. 76). Unlike bottom-water POC, there were no clear depth-related patterns with sediment TOC (Fig. 77).

As stated in Methods, TOC measurements were examined separately at a later date from other test parameters, for purposes of direct comparison against bottom-water POC measurements and as a second trophic indicator. The results of this analysis yielded far fewer statistically significant relationships with TOC than was seen for POC. Only water depth, polychaete abundance dominance, and mean polychaete abundance showed significant correlations. Variables excluded from significant correlations included bottom-water POC (Kendall's t = 0.19).

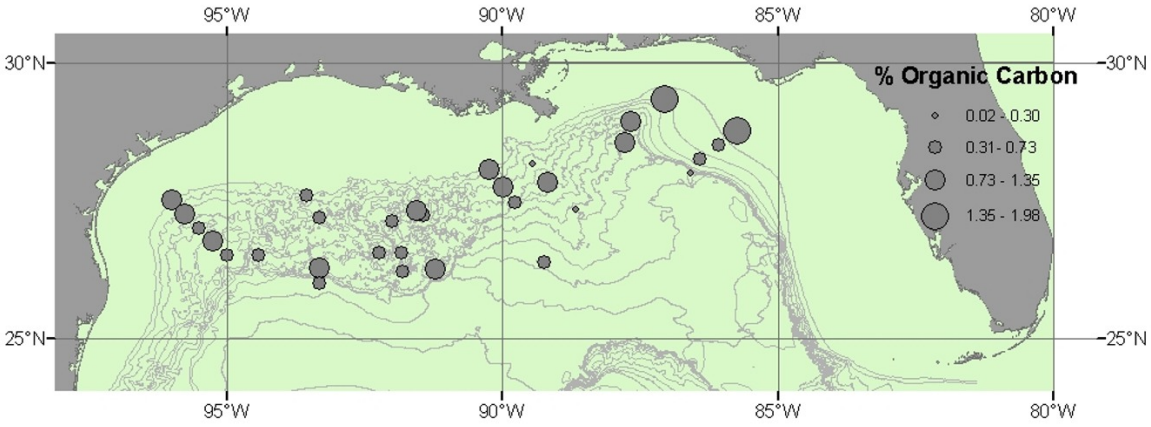

Fig. 76. Sediment total organic carbon values for the northern Gulf of Mexico. Units are expressed as percentages.

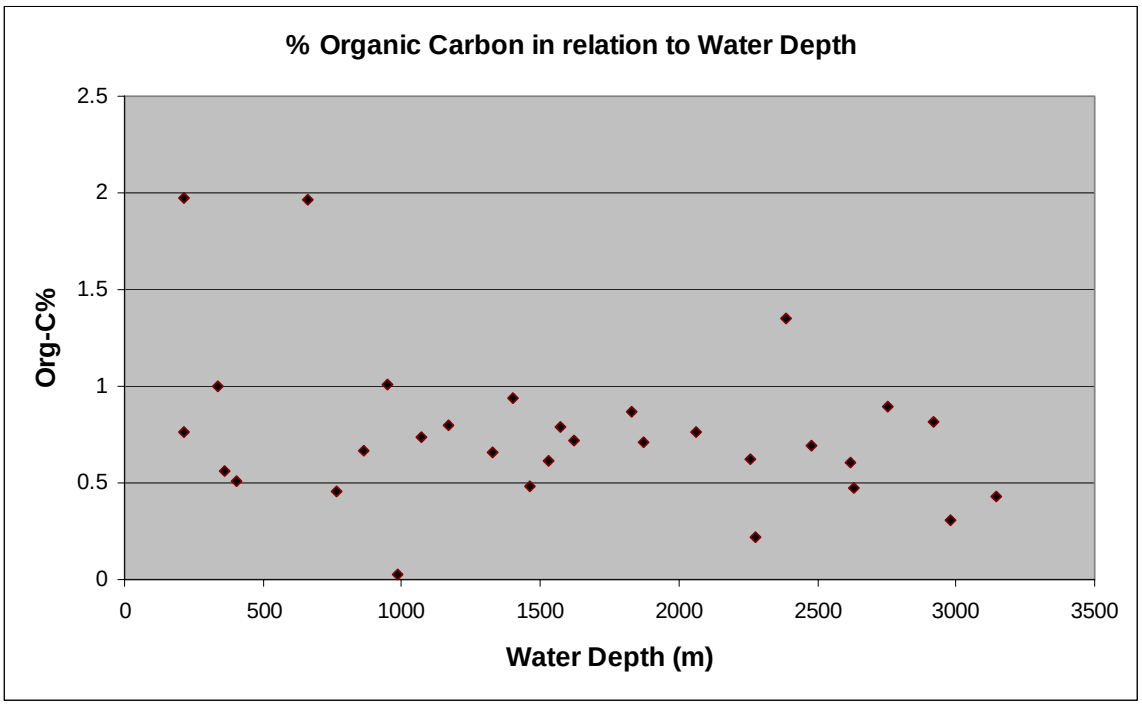

Fig. 77. Sediment total organic carbon in relation to water depth. Although flagged as significant with correlation analysis, TOC relation to water depth was not supported in regression testing.

Only mean polychaete abundance showed a regressional relationship with an r^2 greater than 0.20, and that only when plotted into a curvilinear model (Fig. 78).

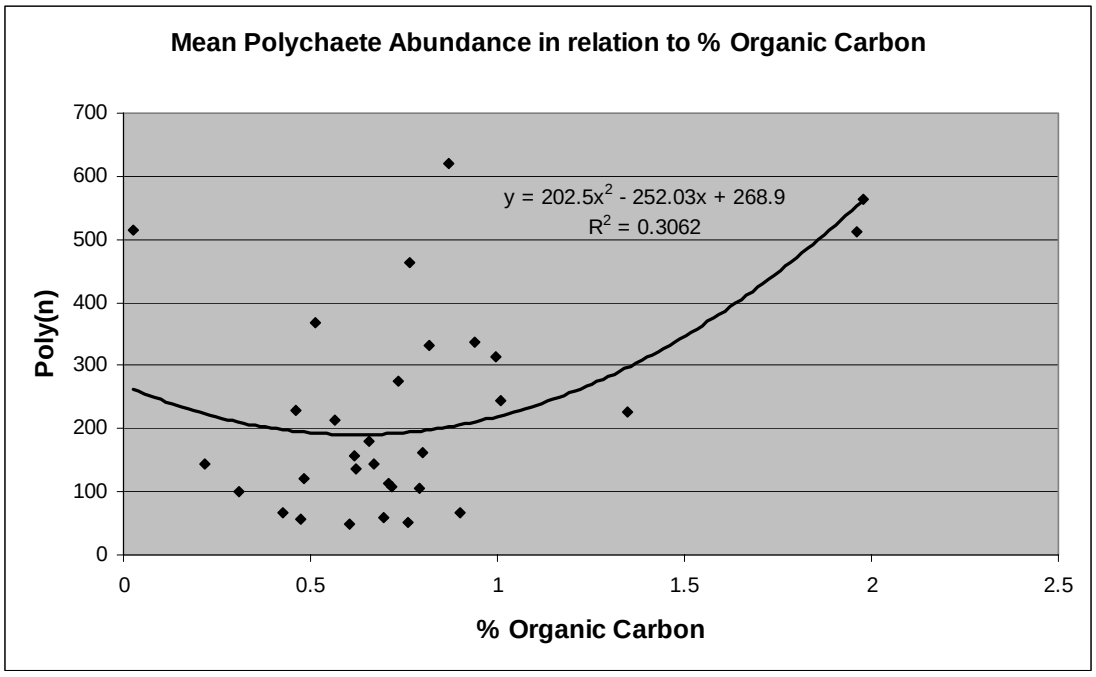

Fig. 78. Mean polychaete abundance in relation to sediment total organic carbon. Abundance values are actual (.1725 m^2). Regression model used is second-order polynomial.

It is likely that the lack of correlations of TOC to virtually all of this study's test variables was a result of the way TOC was sampled. As previously mentioned in section 3.9., sediment nutrients are known to be highly patchy even within individual boxcores. As only one TOC measurement was taken at each DGoMB survey station, the probability that taken values were "average" for a local area (or even a single boxcore) is impossible to quantify. The same holds true for sediment grain size, which was also only taken from one boxcore per survey station (and may also explain the poor correlations found with this test variable).

Indirect support for patchy local-scale TOC can be seen at DGoMB sites where the most surface bioturbation (category 5) was measured. These five stations displayed significantly more variance than less bioturbated stations. Following Hughes et al.

(2005), areas possessing heavy megafaunal burrowing activity would be expected to possess more heterogeneous nutrient patterns than areas less bioturbated.

3.11. Summary of Hypothesis Testing

This section lists the results of hypothesis testing as described in section 1.2.3.. It is broken down by specific test variable.

3.11.1. Community Homogeneity Throughout the Deep Gulf of Mexico

Community homogeneity was determined by simple examination of basin-wide range values of primary biological test variables. Null hypotheses and their results are shown.

H_1: Total macrofaunal mean abundance is similar: **Rejected**

H_2: Macrofaunal functional group (polychaetes, sedentary fauna, motile crustaceans) abundances are similar: **Rejected** (all three groups)

H_3: Macrofaunal functional group abundance patchiness values are similar: **Rejected** (all three groups)

H_4: Macrofaunal functional group abundance dominance values are similar: **Rejected** (all three groups)

H_5: Macrofaunal taxonomic metadiversity is similar: **Rejected**

H_6: Macrofaunal taxonomic beta diversity is similar: **Rejected**

3.11.2. Community Relationships to Environmental Factors

As described in Methods, causal patterns linking macrofaunal community structure to specified environmental factors were determined via regression analysis. Regression values possessing an r^2 value greater than 0.14-0.15 were almost always statistically

significant according to ANOVA analysis (F-value less than 0.05). Values at or exceeding 0.20 always were shown to be statistically significant and so a regressional r^2 of 0.20 was deemed the minimum level for general use by the author (r^2's between 0.14-0.20 were used judiciously on a case-by-case basis so long as they were statistically significant by ANOVA). Values which statistically correlated but did not pass regression testing were not examined in this study. Null hypotheses for community relationships are shown, subdivided by environmental test factors.

A. <u>Water depth</u> is not related to macrofaunal community structure.

H_{01}: unrelated to total macrofaunal mean abundance: **Rejected**; inverse relationship

H_{02}: unrelated to macrofaunal functional group mean abundance: **Rejected** (for all three groups); inverse relationships (also for all three groups)

H_{03}: unrelated to macrofaunal functional group abundance patchiness: Not Rejected (all three groups)

H_{04}: unrelated to macrofaunal function group abundance dominance: Partial Rejection

H_{04a}: polychaete abundance dominance: Not Rejected

H_{04b}: sedentary fauna abundance dominance: **Rejected**; inverse relationship

H_{04c}: motile crustacean abundance dominance: **Rejected**

H_{05}: unrelated to macrofaunal taxonomic metadiversity: Not Rejected

H_{06}: unrelated to macrofaunal taxonomic beta diversity: Not Rejected

B. <u>Sediment Type</u> is not related to macrofaunal community structure.

H_{07}: unrelated to total macrofaunal mean abundance: Not Rejected

H_{08}: unrelated to macrofaunal functional group mean abundance: Not Rejected

H_{09}: unrelated to macrofaunal functional group abundance patchiness: Not Rejected

H_{10}: unrelated to macrofaunal functional group abundance dominance: Not Rejected

H_{11}: unrelated macrofaunal taxonomic metadiversity: Not Rejected

H_{12}: unrelated to macrofaunal taxonomic beta diversity: Partial Rejection

H_{12a}: percent sand fraction: Not Rejected

H_{12b}: percent silt fraction: Not Rejected

H_{12c}: percent clay fraction: **Rejected**

C. <u>Near-Bottom POC</u> is not related to macrofaunal community structure.

H_{13}: unrelated to total macrofaunal mean abundance: **Rejected**

H_{14}: unrelated to macrofaunal functional group mean abundance: **Rejected** (all three groups)

H_{15}: unrelated to macrofaunal functional group abundance patchiness: Partial Rejection

H_{15a}: polychaete abundance patchiness: Not Rejected

H_{15b}: sedentary fauna abundance patchiness: Not Rejected

H_{16c}: motile crustacean abundance patchiness: **Rejected** (inverse relationship)

H_{16}: unrelated to macrofaunal functional group abundance dominance: Not Rejected (all three groups)

H_{17}: unrelated to macrofaunal taxonomic metadiversity: Not Rejected

H_{18}: unrelated to macrofaunal taxonomic beta diversity: **Rejected** (inverse relationship)

D. <u>Sediment TOC</u> is not related to macrofaunal community structure.

H_{19}: unrelated to total macrofaunal mean abundance: Not Rejected

H_{20}: unrelated to macrofaunal functional group mean abundance: Partial Rejection

H_{20a}: polychaete mean abundance: **Rejected**

H_{20b}: sedentary fauna mean abundance: Not Rejected

H_{20c}: motile crustacean mean abundance: Not Rejected

H_{21}: unrelated to macrofaunal functional group abundance patchiness: Not Rejected

H_{22}: unrelated to macrofaunal functional group abundance dominance: Partial Rejection

H_{22a}: polychaete abundance dominance: **Rejected**

H_{22b}: sedentary fauna abundance dominance: Not Rejected

H_{22c}: motile crustacean abundance dominance: Not Rejected

H_{23}: unrelated to macrofaunal taxonomic metadiversity: Not Rejected

H_{24}: unrelated to macrofaunal taxonomic beta diversity: Not Rejected

E. <u>Sediment Bioturbation Intensity</u> is not related to macrofaunal community structure.

H_{25}: unrelated to total macrofaunal mean abundance: **Rejected**

H_{26}: unrelated to macrofaunal functional group mean abundance: Partial Rejection

H_{26a}: polychaete mean abundance: **Rejected**

H_{26b}: sedentary fauna mean abundance: Not Rejected

H_{26c}: motile crustacean mean abundance: **Rejected**

H_{27}: unrelated to macrofaunal functional group abundance patchiness: Not Rejected

H_{28}: unrelated to macrofaunal functional group abundance dominance: Not Rejected

H_{29}: unrelated to macrofaunal taxonomic metadiversity: Not Rejected

H_{30}: unrelated to macrofaunal taxonomic beta diversity: Not Rejected

4. DISCUSSION

4.1. Synopsis of Findings

The results of this study indicate that macrofauna communities in the deep Gulf of Mexico are highly heterogeneous. Wide variation in all macrofaunal measurements, at both local and regional scales, affirms the increasing importance in marine ecology of spatial patchiness in biological communities and the risks in upscaling measurements to larger-sized areas (Valiela, 1995). Values of abundance and diversity at local scales may vary more that those between different regions or depth zones within the Gulf of Mexico.

Seafloor sediment mixing is considerable throughout much of the continental slope and even on the abyssal plain. It is particularly marked in shallower depths and in upper-slope submarine canyons. Macrofaunal abundance is positively associated with sediment bioturbation. Very high bioturbation levels negatively affect population structure of more sedentary macrofaunal taxa.

Indirect measurements of benthic food supply using organic carbon has validity, though within-sediment measurements are far less useful than measurements taken from the overlying water column. The latter values strongly cue with macrofaunal abundance, indicating that deep-sea communities are highly food-limited. Beta diversity measurements in areas where particulate organic carbon is high lend support to the theory that competitive exclusion breaks down in the macrofaunal community in such situations.

Substitution of genus/species-level identifications with those of much higher taxonomic rankings (Phylum, Class, Order) was shown to have little to no value as direct diversity measurement. Although deep-sea benthic macrofauna are very diverse at higher taxonomic levels, evaluation of ecological controlling factors at such levels was ineffective.

4.2. Local-Scale Patchiness of Macrofauna in the Deep Gulf of Mexico

From the two within-site faunal patchiness measurement types used (abundance variances, taxonomic dissimilarity), small-scale habitat structure was evaluated. As described in Methods, abundance variance examined patchiness in faunal *densities* among same-site boxcores, while taxonomic dissimilarity (beta diversity) looked at patchiness of faunal *types*.

4.2.1. Abundance Variance

For polychaete, sedentary fauna, and motile crustacean groupings, intra-site density patchiness tended to be high, averaging 45%, 60%, and 48% respectively. Although no patterns were seen with polychaete patchiness, the sedentary fauna and motile crustacean groups both displayed inverse relationships with one another at the shallow shelf/slope survey stations. Specifically at these shallow locations, sedentary patchiness was very high (>75% except in canyons), and motile crustacean patchiness was never high (<60%). High sedentary patchiness values went hand-in-hand with the highest sedentary *abundances* (>1,500 m^2), and yet sedentary patchiness also appeared to *negatively* affect

the abundance dominance of motile crustaceans (Fig. 35). This is almost certainly related to benthic food supply, as the sedentary fauna were only found in high abundances (>690 m^2) at depths less than 500 m, where more surface-derived POC can be made available to the benthic community than in deeper slope areas. All macrofauna should (and do from the author's data) react towards increased food availability by increasing their densities, but the sedentary macrofauna appear to have the advantage in shallower depths, as evidenced by their heightened dominance fractions exceeding 30% (Fig. 26). However, despite the high ratio of sedentary fauna found at the shelf/slope break, motile crustaceans are still found in large numbers.

Within the DeSoto and upper-mid Mississippi canyons, motile crustacean patchiness values were quite low (<40%) in relation to other survey areas (Fig. 46). And although only crudely examined, crustacean patchiness values were higher in the eastern GoM than the western GoM (Fig. 46).

Elevated abundance patchiness values can be reflective of a number of things. For mobile fauna, high local-scale variation can be an indicator for faunal aggregations based on sporadic food resources (i.e. deadfall), reproduction, or natural migration. (Lauerman et al., 1996; Kaufmann and Smith, 1997). For more sedentary faunas, high local-scale patchiness might presume macrofaunal-scaled habitat heterogeneity, with less mobile or fixed organisms confining themselves around areas of high sediment stability (Rhoads, 1974). For both mobile *and* sedentary macrofauna, patchiness densities can be altered on local scales by megafaunal grazing pressures, such as sediment-sifting

macrourid fishes or “omnivorous” deposit and suspension-feeding megafauna (Marshall, 1979).

There is also the possibility of sampling error to consider. High abundance patchiness is often seen when collection sizes are undersized. High variance can also be indicative of insufficient sampling overall (Jumars and Eckman, 1983). Undersized areal sampling can be explored by varying the size of each collection, while increasing the number of intra-site samples would examine the size of each sample *series* (Jumars, 1975). Unfortunately, neither of these options was exercised, as they were not part of the original DGoMB design, and if they were, would have grossly increased the sampling and analysis efforts (Rowe, personal communication). However, to put things in perspective with similar deep-sea studies (i.e. the earlier NGoMCSS study), the size of the GOMEX boxcorer used in the DGoMB was significantly larger. And although the USNEL 0.25 m^2 boxcorer (or variations of it) is commonly used for many macrofaunal studies, many biologists prefer to extract only the innermost 0.09 m^2 for analysis (i.e. Levin and Smith, 1984; Glover et al., 2001). Therefore, any errors stemming from insufficient DGoMB sampling should be of less concern (in terms of sediment analyzed) over the majority of reported deepwater macrofaunal studies that perform multi-site comparisons.

Jumars (1975) extensively explored within-site and adjacent-site patchiness of polychaetes within the Coronado Sea Fan off of southern California. Using the (new at the time) 0.25 m^2 USNEL spade boxcorer in multiple partitioned and non-partitioned sampling combinations, it was determined that local-scale abundance variance was less

than that observed in shallow-water studies. Jumars theorized that this was likely due to shallow water sampling efforts covering over more physically-generated microhabitat gradients than found in deeper-depth sediment communities. In a later re-examination of deep-sea macrofaunal sampling techniques and results, Jumars and Eckman (1983) listed ten technique-related problems that could contribute to high sample variances (Table 22).

Table 22.
Errors in benthic sampling known to increase abundance variation measurements between samples. Taken from Jumars and Eckman (1983).

1. Active avoidance of, or attraction to, the sampler.
2. Bow-wave effects.
3. Imprecision of area taken by the sampler.
4. Escape or winnowing from the sampler during sample retrieval.
5. Loss during sample removal from the sampler.
6. Variation in retention efficiency during sample washing.
7. Variation in quality of fixation and preservation.
8. Variation in efficiency of animal removal from residual sediments.
9. Errors in identification.
10. Errors in counting, recording, or calculation.

Factoring in such errors, Jumars and Eckman still were of the opinion that small-scale variances in faunal diversity and abundance would still tend to be high. They concluded that non-random dispersion patterns were the norm for macrofaunal populations examined at small-scales, possibly due to habitat partitioning and asynchrony of successional series.

DGoMB macrofaunal collection and analysis procedures were designed to specifically address most of the sampling errors as shown in Table 22. The boxcorer was dropped into sediment only after a brief shipboard delay to verify vertical separation between the sampler and the seafloor. Sediment samples which appeared damaged or incomplete were generally not used (and not at all in the author's study). Animal escape during sediment capture and retrieval was minimized by a fast gravity drop by the boxcorer into the target sediments, and from rapid winching up of the boxcorer almost immediately following seafloor contact. Removal of sediments from the boxcorer was very thorough and even involved extraction of the fauna found in the overlying water layer atop the sediment sample. Sample washing was performed in a uniform manner, as was preservation. Virtually all macrofauna were rough sorted to higher taxon in a central location (TAMU Oceanography Benthic Ecology Laboratory, with all sorting personnel trained and supervised by a senior research biologist (Fain Hubbard). A very few macrofaunal samples were sent to laboratories in Mexico and Louisiana for rough taxonomic identification, but these were either abyssal plain samples not used by the author (Mexico) or samples re-sorted by the central laboratory following quality control concerns (Louisiana).

4.2.2. Taxonomic Patchiness (Dissimilarity): Beta Diversity

Turnover diversity for macrofaunal taxa ranged from 1.27-1.93 (21-48%), averaging 1.51 (34%). Given general community structure patterns for deep-sea macrofauna (high diversity, low abundance), such high taxonomic patchiness values were not unexpected.

Local-scale turnover of taxa showed linkages to numerous factors. POC was the strongest. DGoMB sites with high bottom-water POC tended to have a more homogeneous distribution of macrofaunal taxa (Fig. 56). This would indicate a trophic control; reduced food (POC) supply would keep overall abundances down, fostering a benthic habitat structure with locally reduced diversity (Rex et al., 2005). This is directly supported by comparing taxonomic richness to near-bottom POC (Fig. 75), and also by negative relationships of taxonomic patchiness to all four macrofaunal abundance values measured (total, polychaete, sedentary fauna, motile crustaceans). For these latter four, taxonomic patchiness was seen to decline as they (faunal abundances) went up (Fig. 11). This argues for a local community structure in which competitive exclusion processes resulting from increased food supply are not operating for many (or most) taxonomic groups, at least not at lower POC levels. Given that the majority of macrofauna in the deep-sea are considered being deposit feeders (Jumars and Gallagher, 1982), a lack of competition via trophic partitioning is not surprising.

It is not unreasonable to argue that when total macrofaunal densities attain a minimum level (i.e. 5,000 m^2), more macrofaunal taxa (particularly rare ones) are represented at small-scales. Examination of our richness and abundance measurements supports this (Fig. 79).

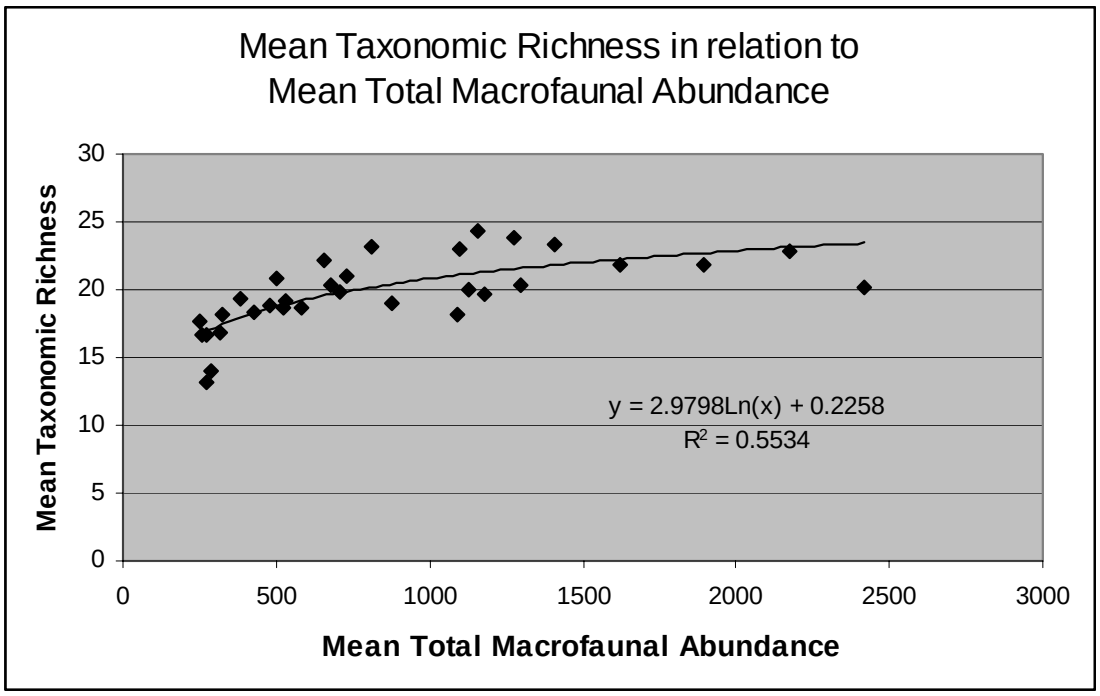

Fig. 79. Mean taxonomic richness in relation to mean total macrofaunal abundance. Abundance values are actual (0.1725 m^2). Regression model used is logarithmic.

The western GoM showed greater taxonomic patchiness than the eastern GoM (Fig. 54), which may be POC-linked (as higher POC seen in eastern GoM). Nearly all (8 of 9) of the sites with the highest patchiness values (>1.58) were located in the western GoM at middle-lower slope depths (>1,300 m). Although not all of these high patchiness areas measured below average (<2.6 uM), none of them were on the high end of the scale (>3.8 uM) either.

As previously mentioned in Methods, the effects of sampling error on within-site patchiness values cannot be discounted. Inherent imprecisions in ship-deployed deepwater boxcores make the dispersion distance between adjacent sample cores difficult to assess. Boxcores taken at deeper depths might be argued to have a wider

dispersion range than cores taken at shallower depths. In the case of our results, higher within-site patchiness was in fact found at many deepwater stations (Fig. 55), although the regressional relationship was poor (linear r^2 =0.19).

4.3. Regional-Scale Differences in Community Structure

Large-scale patterns in macrofaunal community structure for the continental slope regions of the northern Gulf of Mexico were primarily examined via a series of single-measurement test factors among 32 DGoMB survey stations. These measurements included macrofaunal abundance (total and for three ecological groupings), taxonomic richness, taxonomic diversity, bioturbation intensity, sediment POC, and sediment grain size. These test factors were used to both identify regions in the GoM with differing macrofaunal community structures, and attempt to at least partially explain such differences.

4.3.1. Eastern vs. Western Gulf of Mexico

As described in Methods, comparisons between the eastern and western GoM were only crudely examined via subjective visual observations of basin-wide maps of test variables. Overall, the eastern Gulf of Mexico tended to have greater abundances of macrofauna than the western GoM. This was true for the lumped aggregate of all macrofauna sampled, as well as for that of the three ecological groupings. Given the relationships observed between POC and abundance (Figs. 15, 22, 31, 45), and the preponderance of literature coupling macrofaunal densities to organic matter imports

(i.e. Cosson et al., 1997; Levin et al., 2001; Rex et al., 2005), higher DGoMB macrofaunal densities in the eastern GoM were likely linked to the higher near-bottom POC found there.

Unlike abundance, the *community fraction* of sedentary fauna was low (4-13%) in the eastern GoM. A reduced dominance would indicate competitive exclusion by other macrofaunal groups (Rhoads, 1974). Reduced dominance combined with increased overall abundance might be seen in habitats that are *not* food-limited, but are competing for space. In the case of many sedentary macrofauna (i.e. sponges), such loss of space could occur via excessive sediment disturbance (Gray, 1974).

Local-scale taxonomic patchiness was higher in the western GoM, reflecting less homogeneous community structure on microhabitat small scales. Higher POC availability in the eastern GoM may explain this, as it does for macrofaunal abundance. In this case (*reduced* food supply), Allee effects may come into play, whereby local population densities of a species are too low to be reproductively sustainable. Consequently, local extinction occurs. Rex et al. (2005) lists the Allee effect as being a powerful diversity-reducing agent in regions of the deep sea where food supply is very low.

4.3.2. Upper vs. Lower Continental Slope

For purposes of this study, the “lower slope” is loosely defined as regions exceeding 1,500 m down to the abyssal plain, while the “upper slope” comprises depths between 200-1,500 m. In some circumstances the term “mid-slope” is used in reference to depths

roughly between 800-1,500 m. These depth zones roughly correspond to those used by Galloway (1988) for macrofauna.

4.3.2.1. Upper Slope: Faunal Patterns

For total, polychaete, and sedentary macrofauna, abundance was higher at upper slope than at lower slope depths. Much weaker declines with water depth were seen for motile crustaceans, but they followed the same general pattern. Sedentary fauna abundance was highest (by far) in shallow water less than 500 m, and displayed very steep declines at deeper DGoMB stations (Fig. 27). In the NW Mediterranean in and around Toulon Canyon, Stora et al. (1999) also observed a steep drop in suspension feeders at 500 meters, but were unclear as to the proximal causes that brought it about. Ivany et al. (1994) ascribe the loss of upper slope suspension feeders to increasing water depth, decreased mean sediment grain size, and increased sediment organic content. Presumably the heightened sediment organics both foster and alter infaunal bioturbation to a level that elicits a community shift as described by Pearson and Rosenberg (1978). In such cases, deposit feeding trophic groups should dominate. The dominance of one trophic group over another within a community is referred to as “trophic group amensalism”. Rhoads and Young (1970) explain this as the inhibition of one trophic type by another, and have particularly used it in reference to both deposit and suspension feeders within soft-sediment habitats. In the case of the deep-sea benthos, Rhoads and Young predicted three types of macrofaunal communities that would exhibit trophic amensalism against one another. This is summarized by Gray (1974):

(1) Suspension feeders dominating; excluding deposit feeders due to low food supply

(2) Deposit feeders dominating; excluding suspension feeders via excessive sediment reworking and burial

(3) Mixed trophic groups (both suspension and deposit feeders); community diversity brought about by high sediment stability.

Polychaete and sedentary fauna dominances were both higher at upper slope depths, while the reverse was found for motile crustaceans, albeit only at depths shallower than 500 m. It would seem that at these shelf/slope transitional zones, motile crustaceans are at a competitive disadvantage. This may be another example of trophic group amensalism, although in this case the controlling factors are less understood. Gray (1974) gives some examples of "spacing out phenomena", whereby adults display territorial aggression towards one another. However, Gray's examples were primarily megafaunal decapods and tube-building polychaetes. Much smaller macrofaunal crustaceans may not display such complex behaviors. The marked density, patchiness, and abundance reductions of motile crustaceans along the shelf/slope are not something the author referenced in previous deep-sea literature, and deserves future scrutiny.

Abundance patchiness for sedentary macrofauna was very high (>75%) in areas shallower than 500 m, which is unusual given that both mean abundance and community dominance values were high for this group. One plausible explanation that could be given for this is that heavy sediment disturbance in these shallow areas maintained high

local-scale population heterogeneity. Cosson et al., (1997) attribute intra-site patchiness to local-scale faunal aggregation (as a result of increased environmental heterogeneity), but it might also be argued that recent sediment burial could create short-term, depauperate population patches as seen by colonization tray experiments by Snelgrove et al. (1996). Grassle and Morse-Pourteous (1987) refer to such community patchiness as an example of “patchy disequilibria”, which is created by moderate and regular disturbance events.

4.3.2.2. Lower Slope: Faunal Patterns

The lower continental slope possessed reduced faunal abundances for the majority of deep survey stations. One of the few exceptions to this was the lower DeSoto canyon, which maintained faunal abundances equal to or only slightly lower than that found in the upper canyon. It is likely that POC values throughout this particular canyon area are a contributing factor, as values were markedly higher than at most other GoM stations at equivalent water depths (Fig. 74).

Polychaete dominance of the macrofaunal community decreases at lower slope depths to no more than 20%. Sedentary fauna follow a less linear or gradual pattern. After the sharp dominance and abundance decline of sedentary fauna beyond the 500 m contour, these organisms tend to rapidly decline numerically. However, sedentary fauna display a moderate resurgence in community dominance (values mostly between 9-15%) at depths greater than 2,000 m within many western GoM survey stations (Fig. 26). However, while their dominance increases somewhat, their numerical abundance does not.

Increases in dominance of particular taxa are key indicators for differences in community structure (Sokolova, 1972; Cosson et al., 1997). The reduced POC in the lower slope, coupled with the overall macrofaunal abundance declines found there, point to a highly food-limited environment. The importance of bioturbation as a controlling factor is likely much reduced in the lower slope, as faunal abundance patchiness values are highly variable despite marked bioturbation declines. High abundance patchiness values in the lower slope are likely linked simply to scarcity of fauna. This is supported by the trend towards reduced mean taxonomic richness with water depth (Fig. 49), and by the high local-scale taxonomic patchiness also commonly seen in deeper survey stations.

4.3.3. Submarine Canyons

Survey stations were located in three canyons, one small, deep canyon in the western GoM (Alaminos), and two eastern GoM canyons of much larger size (DeSoto, Mississippi), spanning both upper and lower slope depths. Submarine canyon communities often displayed very different characteristics from non-canyon areas at equivalent depths and/or close geographic proximity. The DeSoto canyon in particular is noted for its high macrofaunal densities (> 6,300 m^2) both in upper *and* lower slope depths (Fig. 10), which very likely is linked to the relatively high (>3.2 uM) sediment POC levels found as far down as 2,300 m.

4.3.3.1. Upper Canyons: Faunal Patterns

Both the Mississippi and DeSoto upper canyons possessed higher abundances for total macrofauna as well as for polychaetes and motile crustaceans. Sedentary fauna showed more moderate abundance values, only slightly higher than non-canyon sites at equivalent depths (Fig. 29). Polychaetes displayed a gradual depth decline in the Mississippi canyon, which would have thought to be attributable to decreasing POC levels as other DGoMB site comparisons and the deep-sea literature (i.e. Cosson et al., 1997) suggests. However, sediment POC in the Mississippi canyon did not display steady depth declines. This is unusual, and probably has something to do with properties of the canyon itself. Like most submarine canyons, the Mississippi canyon's steeper depth gradient (relative to adjacent continental margins) should cause it to behave like a regional funnel for allochthonous sediments, detritus, and other particulate matter. Continuous or episodic gravity-driven movements of this material are more likely to mix surface sediments and near-bottom water masses throughout a canyon at a faster rate than on a large continental slope, thus making benthic water mass particulate measurements at different canyon depths more homogeneous.

During the summer of 2001 (a year after the macrofaunal collections used in this study were taken), bottom current measurements were taken at stations MT3 (upper canyon) and MT6 (lower canyon) using a moored ADCP. The upper canyon site measured bottom currents of 2.5 cm/second, and the lower canyon 5.0 cm/second (Rowe, in review). This is considered too weak to erode the seabed (Levin et al., 2001), although with such a short monitoring time (less than three days), it is possible that

stronger currents can occur. Indeed, given the nature of the sediments throughout the entire canyon, and our knowledge of the hydrodynamic regimes found in other submarine canyons (Gage, 1997), at least periodic high current periods must take place. Unlike other regions of the deep GoM, the sediments of the Mississippi canyon are primarily of terrigenous origin, specifically deriving from the Mississippi River (Balsam and Payne Beeson, 2003). The carbonate levels in particular are extremely low (<10%). Although the author did not examine the role (if any) of high carbonate content on macrofaunal community structure, nor that of terrestrially-derived sediments, the fact that the lower canyon possesses such sediments indicates for a significant transport mechanism.

Generally, polychaete abundance and bioturbation intensity were closely correlated throughout the GoM, but usually POC was also correlated to bioturbation. That POC did not in the Mississippi canyon indicates that POC is a less useful trophic indicator here, or that trophodynamic processes operate differently. Levin et al. (2001) discuss how seafloor areas modified by recent large-scale sediment disturbances can dramatically alter benthic community structure. Where a massive turbidite swept through the Madeira Abyssal Plain, for example, polychaete diversity and abundances was reduced, and the group's dominance over other macrofauna was heightened. Granted that this site was far more of an oligotrophic environment than that of the upper Mississippi canyon, so polychaete community structure should hardly be expected to be similar. What is important is that regions that experience or have recently experienced large-scale

sediment disturbances should differ markedly in community structure from adjacent, non-disturbed areas.

Sedentary fauna were less conspicuous members of canyon communities, even in lower slope areas (Fig. 26). Although their densities were at least 350 m^2 except at the very deepest lower slope sites, community dominance values were far lower, representing less than 8% in all canyon sites except one (MT5), which was still on the low side (14%) relative to other regions of the GoM. In the POC-rich DeSoto canyon, sedentary dominance values at all three survey stations were less than 5%. Motile crustaceans and polychaetes only partially filled in the gap created by reduced sedentary fauna, which means that other macrofaunal taxa had heightened dominance as well.

Although macrofaunal studies within submarine canyons are rare in the literature and almost always focus on deposit feeding groups, Stora et al. (1999) examined suspension feeding taxa (in addition to other nutritional modes) in the Toulon canyon within the NW Mediterranean. A complete disappearance in suspension feeders was observed within the canyon axis at the 500 m contour. Sample sites at taken at equivalent depths on the continental slope to the left and right of the canyon however, retained small (< 6%) fractions of suspension feeders down to at least 1,500 m. Stora et al. theorized that the canyon funneling effect created an environment (higher organic deposition, increased bioturbation) within Toulon canyon unsuitable for suspension-feeding lifestyles. Within the upper Mississippi and DeSoto canyons, similar patterns (reduced dominance) were seen for sedentary fauna. Heavy bioturbation activity and high sediment organic

carbon (and to a lesser extent, POC) support a benthic habitat structure ill-suited for this trophic group.

Local-scale patchiness abundance of motile crustaceans was very low relative to other GoM stations (<40%) in the upper Mississippi and throughout the entire DeSoto canyon (Fig. 46). These same areas were among the more highly bioturbated in the GoM, and although POC content did not perfectly match bioturbation intensity, near-bottom POC in four of the five sites was still on the higher end (>3 uM) compared to other test stations (the exception being MT4, 2.6 uM). Further, motile crustacean abundance was high if not very high (>1,200 m^2). This combination of high bioturbation, high crustacean abundance, low crustacean patchiness, and elevated POC argues for a benthic community that frequently undergoes disequilibrium from sediment and/or grazing disturbance (bioturbation, abundance), but not necessarily pulsed nutrient imports (patchiness, POC). Although the author could not locate any previous studies of macrofaunal crustaceans within submarine canyons, these animals are typically well adapted for sediment disturbance and can disperse readily (Gage and Tyler, 1991). Their very low abundance patchiness values may be indicative that megafaunal grazing intensity is high. High megafaunal biomass collected from DGoMB trawls in these areas supports (albeit anecdotally) this.

What is most puzzling are the very low abundance patchiness values seen for this group within these canyon sites. Fig. 47 indicates that Gulf-wide, lower POC correlates with lower abundance patchiness. But in the DeSoto and upper Mississippi Canyon, this pattern is reversed. As members of this group (particularly epibenthic fast-walking or

swimming types) should tend towards aggregative behaviors around localized food sources (Gage and Tyler, 1991), there should be high local-scale abundance patchiness in these submarine canyons, not low. It may be that the crudity of the lumped crustacean grouping used in this study is to blame. If crustacean abundance values at these sites are being dominated by a particular group or groups that disperse very evenly, it could mask out the signals from the remainder of crustaceans. A likely scenario in which this could take place would be a synchronized reproductive event of particular species. Seasonal and/or food supply-cued reproductive events have been observed in a variety of deepwater macrofaunal crustaceans (Cartes and Sorbet, 1996; Kaim-Malka, 1998; Cartes et al., 2001).

4.3.3.2. Lower Canyons: Faunal Patterns

Lower canyon sites (excepting the DeSoto canyon) had very low macrofaunal abundances, and the community structure more closely resembled that of non-canyon lower slope areas. POC was not high (<4 uM), and bioturbation intensity (excluding DeSoto canyon) was moderate (category 3) at best. Taxonomic patchiness was above average to very high, and all three faunal abundance patchiness measurements tended to be high in the Alaminos and lower Mississippi canyon as well. Abundance patchiness appeared to be inversely related to mean abundance at these three survey locations, as did taxonomic patchiness to total macrofaunal abundance. Such inverse relationships could be ascribed to simply an artifact reflecting the scarcity of organisms, and has been observed for megafaunal ophiuroids (Gage and Tyler, 1991). A second explanation is

more circumspect, and involves spatial segregating of fauna as described under more classical equilibrium-type diversity models (stability-time and habitat heterogeneity). Where bioturbation intensity and nutrient imports are reduced (i.e. these lower canyon sites), any existing micro-scale sediment heterogeneity would be expected to persist over long time periods, and act as a habitat partitioning force (Grassle and Sanders, 1973). The problem supporting this was threefold. First, while high sediment stability as indicated by a large sand fraction was observed in the lower Mississippi Canyon, it was not in Alaminos Canyon. Second, for a high signal for local-scale patchiness to be a result of spatial partitioning created by megafaunal lebensspurren or other surface features, there should be significant amounts of surface features locally available. While seafloor photographs at the Alaminos canyon site (AC1) supported this, the lower Mississippi canyon sites did not (although the large amounts of ironstone at these two locations might substitute for this). Third, it was impossible for the author to make age determinations for any epibenthic surface features. With all of these unknowns or non-similarities between lower canyon characteristics, arguing for an equilibrium-driving process is tenuous.

Regarding faunal abundances, motile crustacean counts in the lower DeSoto canyon were *three times* those measured in either the Alaminos or lower Mississippi canyons. Key differences of the lower DeSoto canyon are the higher organic carbon values (both near-bottom POC and sediment TOC), and higher bioturbation intensities. As the linkage between standing stocks and organic carbon inputs is one of the better established patterns known for macrofauna (Levin et al., 2001; Rex et al., 2005), and the lower

DeSoto canyon sampled much higher total macrofaunal abundances than other lower-slope DGoMB sites, it is very likely that elevated organic carbon is the delineating factor separating basic community structure differences between the lower DeSoto canyon with that of the Alaminos and lower Mississippi canyons.

4.3.3.2.1. Ironstone in the Lower Mississippi canyon

The sediments sampled at both lower Mississippi canyon sites (MT5, MT6) contained large quantities of red-colored, flattened rocks termed “ironstone” by DGoMB program scientists. Although this material’s sediment coverage was not quantifiably measured, it is probable that ironstone deposits significantly altered benthic community structure. The shingle-like manner in which it lay atop sediments would act as an inhibitor on megafaunal burrowing (evidenced by low bioturbation values at both stations). Further, the sediment sand fractions were very high (> 38%) at these sites, supporting the premise for enhanced sediment stabilizing regimes. Out of all canyon sites examined, stations MT5 and MT6 contained the highest dominances of sedentary fauna. Presumably such dominances are supported by increased availability of hard attachment substrates, reduced burial activity, or a combination of both. In effect, the disturbance processes seen in the upper canyon are counteracted. The macrofaunal communities living in these unusual areas may share greater affinities to those observed in upper-slope regions of the Antarctic (Diaz, 2004) or abyssal plain manganese nodule habitats (Mullineaux, 1989). The effects of ironstone on the benthos within these deep Gulf of Mexico sites may be considerable and merits further study.

4.4. Bioturbation in the Deep Gulf of Mexico

The results of our photographic analysis showed the sediments of the GoM continental slope to be highly bioturbated, particularly far more so than was originally expected for lower slope and abyssal plain regions (Heezen and Hollister, 1971). Later perusal by the author of GoM seafloor photographs taken throughout the mid-late 1960's (Pequegnat, 1983) appeared to support that the GoM continental slope is in fact quite heavily bioturbated even at lower depths, but this was not rigorously examined. Most of our survey stations fell into category 3 or higher, which was our test ranking for "moderate" sediment disturbance. Only two DGoMB study sites met criteria for "very low" sediment mixing (category 1), although "low bioturbation" (category 2) was well represented. Less bioturbated areas were generally found at lower slope depths, while heavily disturbed areas were most commonly encountered at upper slope depths. Heavily bioturbated sites were also found throughout the upper Mississippi and both upper *and* lower DeSoto canyon, as well as both shallow and deep sites on the Florida Escarpment.

4.4.1. Effects of Bioturbation on Benthic Community Structure

Test factors statistically correlated to bioturbation intensity (Table 18) included water depth, bottom-water POC, and abundances for polychaete, motile crustacean, and total macrofauna. With the exception of water depth, all of these were positive regressional relationships.

Even more useful is Table 19, which for each bioturbation category, summarizes the mean measurement values of each test factor statistically linked to bioturbation. From

this, direct comparisons of faunal abundances, water depths, and POC levels can be made in relation to bioturbation intensity.

This study's results clearly show that bioturbation intensity is linked to macrofaunal community structure. Mean abundances for polychaetes, motile crustaceans, and total macrofauna steadily increase in relation with increasing bioturbation, being roughly four times higher between category 1 and category 5-ranked survey stations. Motile crustaceans are almost six times higher. The increases for sediment POC are not as continuous, but category 4 and 5 stations tend to be at least 60% higher than seen for category 1. The author's interpretation of these results supports trophic controls for as being the primary limiting factor for most macrofauna.

Sedentary fauna were a special case. Like the other macrofaunal test groups, they also steadily increased in mean abundance with increasing bioturbation; in fact they spiked seven times higher between category 1 and category 4. But unlike the pattern seen for other macrofauna, mean sedentary faunal abundance peaked at category 4, and then sharply dropped in category 5 locations. In fact, the abundance values for "very high" bioturbation (category 5) for sedentary fauna were one-third that measured on average for "high" bioturbation (category 4) sites, placing them only slightly higher than abundance values for "low" bioturbation (category 2). The author's interpretation of this pattern for sedentary abundance is that benthic areas with highly disturbed sediments act as inhibitors on sedentary macrofauna, as shown by Roads (1974) and Kropp (2004).

The effects on bioturbation on macrofaunal *diversity* test factors were minimal. No statistically significant correlations were found. Even looking just at mean test values

across bioturbation rankings, it is difficult to interpret any patterns at all (Table 23). It is highly possible that the limited usefulness of higher taxa diversity measurements may have prevented any *species-scale* diversity patterns from being more evident.

Table 23
Summary of dominant averages of diversity-measuring test variables in relation to bioturbation intensity. *None* of these were statistically supported by regression analysis. DGoMB stations lacking complete data sets (i.e. abyssal JSSD stations, MT1, MT2) are omitted.

Surface Bioturbation	Very Low (1)	Low (2)	Moderate (3)	High (4)	Very High (5)
Taxonomic Patchiness (beta)	1.7579	1.462	1.578	1.443	1.4986
Taxonomic Metadiversity (H')	6.915	7	7.059	6.555	6.4667
Mean Taxonomic Richness	17.9	19.467	17.9	21.1	20.833
Pooled Taxonomic Richness	31.5	28.333	27.88	30.4	31.167

4.4.2. Abyssal Plain Bioturbation

Five abyssal plain sites were sampled during the DGoMB IIIB cruises in August 2002. Benthic photographs from four of these sites were evaluated in the same manner as used for the DGoMB I survey stations. Oddly, these very deep areas were evaluated as falling under bioturbation criteria for categories 2-4 ("low", "moderate", "heavy"). We originally theorized that abyssal plain regions would display among the lowest bioturbation values, due to their reduced POC and megafaunal abundance levels. That they did not is somewhat baffling. Abyssal plain photographs taken by Heezen and Hollister (1971) throughout various oceanic basins show that such areas tend to display few sediment disturbance features. 1960-era abyssal plain photos within the Gulf of Mexico also show minimal bioturbation throughout multiple sites (Pequegnat, 1983).

The author submits two possible explanations for the elevated abyssal plain bioturbation measurements. The first is simply that with only four abyssal plain sites examined (one of which lay beneath the Mississippi Fan), there was inadequate representation of the Sigsbee Abyssal Plain. A second explanation reflects unbalancing in the author's visual examination procedure due to the way bioturbation was evaluated. Specifically, that the age of lebensspurren could not be determined. As mentioned in Methods, the primary biogenic features used by the author to rank surface bioturbation were large megafaunal-derived mounds and burrows. These were selected over other "categories" of lebensspurren (listed in Gage and Tyler, 1991) due to their greater implied sediment mixing (i.e. Smith et al., 1993; Kaufman and Smith, 1997; Hughes et al., 2005) and their associated creation of benthic micro-scale heterogeneity (i.e. Rhoads, 1974; Aller and Aller, 1986; Smith et al., 1986). Unlike shallow water soft sediments where both biological and physical sediment reworking processes obliterate non-maintained biogenic features rapidly, such features in deepwater environments have much longer residence times, on the order of weeks, months, and in some cases even years (Gage and Tyler, 1991). Thus, it is very possible that many of the mounds and burrows seen in DGoMB survey photographs could have been very old.

The author's inability to age bioturbation features could have led to the reporting of "false positives" among DGoMB seafloor images, particularly at deeper and/or more physically stable sites where long-term persistence of surface features is more likely. The category 5, low-POC survey station S41 at the bottom of the Florida Escarpment is one such candidate area.

4.5. Measures of Benthic Food Supply

4.5.1. POC

Particulate organic carbon was initially selected as the primary trophic indicator due to it being the dominant source of organic matter in deep-sea sediment communities (Morse and Beasley, in review), and that it is known to be a direct nutrition source of deposit and suspension feeders and an indirect one for macrofaunal carnivores and scavengers (Marshall, 1979). Further support for POC as a valid trophic measurement comes from many sources over the last 20+ years, some of the more recent including Levin et al., (2001), Glover et al. (2001), and Tselepides and Lampadariou (2004). Typically, POC (and other measures of nutrient/food) have been used to examine patterns of community abundance. However, trophic measurements have also been used in diversity and dominance studies. Some of these are summarized in Levin et al. (2001).

POC is only one form of particulate organic matter (POM). Other types include more discrete macroscopic particles (i.e. faecal pellets, exoskeleton molts, planktonic forams, eggs), which were not examined in this study. POC generally consists of protein and carbohydrate flakes and aggregate retained on a 45 uM filter (Macdonald, 1975). Often this material clumps and combines with other forms of POM to form macroflocs or “marine snow”. Only about 20% percent of POC is directly usable for heterotrophic nutrition (Gordon, 1970), and this value decreases over exposure time in the water column. Sinking rates of POC are generally quite low, averaging less than 1 meter per day (Riley, 1970). At such slow rates, surface-derived organic particles often take months to years to reach the deep-sea bottom, making it problematic to link seafloor

POC imports with the actual surface waters directly responsible for creating them. Macroflocs are known to sink at least an order of magnitude faster (Gage and Tyler, 1991), but discerning how much surface primary production remains as discrete POC vs. clumping into larger aggregates is difficult to predict.

Unlike other variables used in this study, POC was not sampled from the sediments, but rather from the immediately overlying water column. As such, it could be argued that this measurement did not directly reflect POC content within the actual boxcore samples. However, it can also be argued that by sampling the overlying water mass rather than the sediments containing the macrofauna, concerns regarding local-scale patchiness would be minimized. As shown by Aller (1997) and Hughes et al. (2005), direct and indirect sediment mixing created by benthic fauna can create significant small-scale heterogeneity of nutrients, even within areas contained by a single boxcore. Such patchiness can confound macrofaunal community analysis, particularly if sediment chemistry samples were taken from inside megafaunal burrows containing significant amounts of faecal material and/or sequestered phytodetritus (Hughes et al., 2005). This sampling variability can be greatly reduced by substituting POC samples from the water mass overlying the sediments, rather than taking measurements from the sediments directly. As most of the deep-sea POC is derived from surface falls (Gage & Tyler, 1991), it is to be expected that organic matter found in deepwater near-bottom and nepheloid layers acts as a readily available nutrient source for epifaunal deposit and suspension feeders and scavengers, and a near-immediate nutrient source for most infauna.

4.5.2. TOC

Total organic carbon was also selected as a trophic test variable in this study. Unlike POC, which was sampled from near-bottom waters, TOC was taken directly from sediment samples, specifically, from one boxcore per survey area. Although Morse and Beasley (in review) examined TOC (including carbonate-free TOC) collected from DGoMB samples, their measurements did not correspond to values reported in the program report's raw data (the data used in the author's study). As such, Morse and Beasley's findings regarding TOC relationships to benthic community structure were not referenced. The author's own findings regarding sediment TOC (summarized in section 3.10) found it not to be a useful measurement, but acknowledge that this may reflect inaccuracies due to high sediment pore-water patchiness within single-core samples, as noted by Aller (1997).

Levin and Gage (1998) compared macrofaunal diversity values with sediment organic carbon from various deepwater studies around the world. They found that sediment organic carbon was a "poor" proxy for a food supply measurement, but noted that it correlated with polychaete community structure (even better than total macrofauna). The best correlation was with diversity. Polychaete dominance was observed to increase with organic carbon, but polychaete evenness showed an inverse relationship. From this, Levin and Gage (1998) argued that organic enrichment would favor certain opportunistic polychaete taxa. The author's data shows some support for this, specifically in that polychaete abundance was seen to positively respond to increasing sediment TOC levels (Fig. 78).

4.6. The Importance of Sediment Particle Size

Although sediment particle size has been reported to affect macrofaunal diversity and distribution (Jumars, 1975; Etter & Grassle, 1992), our study found very few relationships. There were some indications that coarser sediments may have had a detrimental effect on motile crustaceans (Figs. 38, 41), or enhanced sedentary faunal dominance (Fig. 28) but these could not be well supported with the data available to us. The broadness of our diversity test factors may have had a role in diluting the sensitivity of our taxonomic-based analyses (Fig. 59); another possibility is simply that too many DGoMB survey sites possessed similar grain size ratios, making site-to-site comparisons very difficult. Only a handful of survey stations possessed sand fractions greater than 25%, and silt:clay ratios were usually within the 1:2 - 4:5 range. Etter and Grassle (1992) used a much more refined sediment analysis technique, which may have permitted them to isolate more finescale patterns among the macrofauna. Levin and Gage (1998), who used similar percent sediment particle size comparisons as the author, also noted a lack of correlations with macrofaunal community structure. Their only reported significant correlation was with crustacean richness and percent clay content (a positive association) in deep Indo-Pacific waters. This happens to fall into line with the author's (non-statistically supported) observations of the motile crustacean group's abundance and abundance dominance being negatively affected by sediments possessing higher sand content.

4.7. Using the Benthic Boundary Layer in *lieu* of Direct Sediment Measurements

A characteristic feature of most deep-sea bottoms is the benthic boundary layer (BBL), also known as the nepheloid layer. This water mass lies directly above the seafloor, and is typically "thinnest" in areas where bottom topography is flat, and vice-versa (Kropp, 2004). The BBL tends to be very rich in surface-derived organic matter, which can favor epibenthic suspension and particle feeders. Carney (2001) believes that due to its role in entraining organic materials, the BBL is intrinsically linked to the benthos, and both should be studied as a cohesive ecological unit.

The BBL also holds attraction as an effective place to take nutrient and chemistry measurements. As noted in sediment biochemistry studies by Aller (1997) and Hughes et al. (2005), values are often highly heterogeneous within very small areas (i.e. a single boxcore). This heterogeneity is enhanced by deep bioturbation activity. As it is not usual for biologists to take more than one biochemical sample per sediment sample, it is quite possible that such biochemical samples are not fully representative of the area. Bioturbation-created nutrient patchiness can however be alleviated by substituting measurements taken in the BBL instead of within the sediments. Being a discrete water mass rather than pore water, the BBL is far more likely to be at least locally homogeneous regarding its dissolved and particulate chemical composition. And due to its proximity to the sediments and direct use by at least some of the epibenthic fauna, the BBL should be a good "proxy site" for taking benthic nutrient measurements.

Such differences in sampling location might explain how this study's POC values correlated much better to test measurements than TOC. POC measurements were taken

from the water directly over the sediments (roughly where the BBL should be), while TOC was taken from a single sediment sample. If the sediment samples were as locally patchy as seen by Aller (1997) in the Nova Scotian Rise, it can be argued that taking single-sample biochemistry measurements is unreliable for use as a community test variable.

The lack of predicted correlations with sediment TOC might also have been confounded by this study's test design. For most DGoMB survey stations, only one sediment sample from a single boxcore was analyzed for TOC. But the present study used the mean of five within-site boxcores to calculate macrofaunal abundance values. Only one of these five boxcores thus was sampled for TOC, but used to represent sediment TOC for the entire local area. It may be possible to examine whether or not such TOC subsampling was better linked to the macrofauna in the boxcore from which TOC was actually taken, versus the macrofauna of adjacent boxcores. This would be done by isolating the specific boxcores from which sediment chemistry samples were taken and running hypothesis testing using the macrofauna specific to those boxcores only. However, this was not done due to time constraints and that TOC was late-added into the author's study as a secondary test measurement.

4.8. Equilibrium Diversity Processes

As described in Section 1, equilibrium-process theories assert that communities exist at/near carrying capacity, driving diversity towards increasingly specialized biota. Such

specializations can be trophically or spatially motivated. This study focused on the latter (spatial specialization), which falls under the habitat heterogeneity model.

4.8.1. Habitat Heterogeneity

The habitat heterogeneity hypothesis postulates spatial variability and environmental stability as being the proximal diversity agents for benthic macrofauna. However, due to the size of the animals involved, such variation in their habitat structure occurs at centimeter spatial scales (Jumars, 1975). Much of this micro-habitat variation is believed to be created via burrowing activity from much larger megafauna. Several studies have examined the effects of deep-sea burrows on sediment structure, most of which have been recently summarized or listed by Hughes et al. (2005). Typically such studies involve removing large sediment cores intact and mapping their three-dimensional structure using vertical sectioning, chemical tracers, or x-ray imaging. Very often, burrowing megafauna will directly enrich pockets of sediment with nutrients (i.e. fecal matter), or indirectly induce the creation of such pockets via forming sediment depressions or holes which collect detritus (Aller and Aller, 1986).

Epipelic (living atop sediment) macrofauna can take advantage of biogenic features by aggregating in micro-scale areas which suit their lifestyles. In shallow-water sediment communities containing mounds formed by the holothuroid *Molpadia oolitica*, suspension-feeding polychaetes preferentially settled on the mounds while avoiding adjacent sediment depressions (Rhoads, 1974). Within the Coronado Sea Fan, surface mudballs produced by one cirratulid polychaete species acted to exclude a paraonid

polychaete species (Jumars, 1975). Along the upper continental slope off North Carolina, Schaff and Levin (1994) found that the paraonid polychaete *Levensenia gracilis* preferred living in surface pits, and infaunal anemones had lower densities on mound sediments. At meiofaunal scales, nematode worms have been found to aggregate within the troughs formed by sand ripples (Hogue and Miller, 1981).

In areas where biogenic features are eroded away by high bottom currents, it is to be expected that epipelic macrofauna are less common. Thistle and Wilson (1996) tested this by comparing population structure of infaunal versus epifaunal isopods at deep-sea sites that were either physically quiescent (stable) or exposed to intermittent erosive currents (unstable). Thistle found that in seafloor areas exposed to strong current regimes, epifaunal isopod populations (and diversity) were far lower than at more quiescent locations.

On large regional scales, Etter and Grassle (1992) compared macrofaunal diversity to that of sediment particle size diversity along the continental slope of the eastern United States. They found significant positive correlations of diversity with silt sediment diversity, and suggested a direct causal relationship.

The functional difference separating sediment variability between the habitat heterogeneity hypothesis and disturbance-type theories is that sediment structure must be stable over long periods of time to fall under habitat heterogeneity models. The author's study examined habitat heterogeneity by attempting to correlate surface bioturbation intensity to late-successional macrofaunal communities. Equilibrium-based theories assert that communities must be at/near carrying capacities. Kropp (2004) summarizes

the successional stages of soft sediment macrofauna. Initially, the community is rapidly populated by a limited variety of generalist opportunists (i.e. certain polychaetes). Following the opportunists are (shallow-burrowing) infaunal deposit and suspension feeders. Following them, the final "equilibrium" stage is reached with the introduction of deep-burrowing deposit feeders.

Sediment stability was assessed by looking at bioturbation intensity and macrofaunal abundance patterns. Sedentary faunas are known to be out-competed by heavy sediment burial activity (Kropp, 2004), therefore a community with both a high dominance of sedentary fauna and a reduced bioturbation ranking could be inferred to represent a more environmentally stable (if successionally "intermediate") community. From this study's results, the dominance (and abundance) of sedentary faunas was highest in areas where bioturbation was intensity was low. And unlike total macrofauna, polychaete, and motile crustacean abundance patterns which were statistically correlated with bioturbation intensity (Table 18), sedentary faunas were not. The author views this as support for the intermediate-stage successional community described by Kropp (2004).

The author used multiple methods to ascertain whether or not a local macrofaunal community was at or near carrying capacity. Ironically, some of these methods (i.e. taxonomic diversity) were the same ones used to argue disequilibrium-based processes. Such similarities point out a major problem of deep-sea biodiversity studies, that is, depending upon indirect or proxy measurements to support hypothesis testing. In the author's case, measurements for carrying capacity using faunal abundances could be interpreted as supporting both equilibrium and disequilibrium models.

Better determinations for carrying capacities were designed around measures of diversity, namely the higher-taxon diversity and taxonomic beta diversity measurements. However, the higher taxon diversity approach proved unworkable. Beta diversity was more useful, yielding significant relationships (Table 12) with numerous test factors. Unfortunately, bioturbation was not one of these, and with no other diversity measurements for taxonomic patchiness to compare against, all of the other correlations could be argued to support both habitat heterogeneity and disturbance-type models. Judging from the inconclusive nature of most of the few studies on deepwater equilibrium processes (summarized by Carney, 1997), this inability to separate the two processes is common.

One of the few sediment particle size correlations made was with beta diversity, showing high taxonomic patchiness occurring with very high clay content levels (Fig. 59). Etter and Grassle (1992) found that silt correlated best with diversity (a positive relationship), although their techniques examined sediment diversity rather than particle-size ratios. The results of the author's study imply the reverse, that a high silt (>60%) environment restricts macrofaunal diversity. This is supported by a review by Gray (1974) for shallow-water sediment communities. He observed that in studies comparing diversity to sediment type, sediments producing high "mud" content had the lowest diversity values as opposed to those sediments possessing coarser particles.

Habitat heterogeneity has neither firm support nor denial in the literature. Perhaps some of the best pro/con studies have been from Kukert and Smith (1992) and Shaff and Levin (1994). Kukert and Smith's observations of selective macrofaunal colonization of

sediment mounds, and heightened species diversity in such mounds over time, lends support for the habitat heterogeneity model. Conversely, Shaff and Levin's examination of macrofaunal communities within sediment mounds and pits yielded few differences with that of undifferentiated sediment areas.

4.9. Disequilibrium Diversity Processes

As opposed to environmental stability-based, equilibrium diversity models, *dis*equilibrium models are governed by disturbance, either environmental, biological, or a combination of both. Studies testing disequilibrium models are more common in deep-sea research. Primarily, this is because they are far easier to implement. Faunal abundance measurements factor more heavily into such theories, as do environmental variables such as food supply. Equilibrium-based theories, on the other hand, require more refined sampling of biological processes, such as individual species-level or functional group responses.

To examine disequilibrium-based processes in the author's study, faunal abundance and trophic measurements complemented direct diversity measures and bioturbation intensity. Thus, more variables could be brought to bear on test hypotheses. The author examined two related forms of disequilibrium theory, biologic disturbance and intermediate disturbance.

4.9.1. Biologic Disturbance Theory

Unlike habitat heterogeneity theory, biologic disturbance theory has gone through multiple evolutions since its initial inception in the early 1970's (Dayton and Hessler, 1972), and is somewhat better understood, primarily due to greater research effort. However, tracking the process of this evolution can be quite difficult as individual researchers tend to have their own "pet titles" for their particular interpretations and applications of this model (i.e. "cropper", "productivity", "contemporaneous disequilibrium", "patchy disequilibria"). This often results more in reader confusion than theory clarification. To avoid this issue, the author limits the review of biologic disturbance theory to more recent published literature summaries on the topic written by well-known deep-sea biologists. These include Gage and Tyler (1991), Gage (1997), Carney (1997), and Levin et al. (2001).

Biologic disturbance originally was designed around the premise that macrofaunal populations (and also diversity) were ultimately controlled by grazing pressures from megafauna (Dayton and Hessler, 1972). Although simple in theory, it was very difficult to test. A poor understanding of megafaunal diet, behavior, and abundance, combined with quantitative sampling problems, made direct grazing calculations a chancy proposition at best (Gage and Tyler, 1991). Many megafauna (i.e. elasipodid holothuroids) were indiscriminant deposit feeders that would slurp up macrofauna just as easily as detritus. Others were known to be more particular (i.e. neogastropods), but were much more difficult to capture in trawls (often passing through the mesh) or too small to resolve in photographs. Use of stable carbon and nitrogen isotopes have the

potential to dramatically improve knowledge about the trophic preferences for many "omnivorous" megafauna (Iken et al., 2001), but this may vary based on food supply.

The complications of working with megafauna led to the use of indirect means to ascertain standing stocks, namely measurement of organic carbon supply to the benthos. The shift from megafauna to benthic food supply permitted much more quantitative measurement ability at varying spatial and temporal scales, and most disequilibrium models now incorporate trophic variables as diversity-controlling factors. Correlations between organic matter flux and macrofaunal populations have been seen to be so strong, Rex et al. (2005) reason that the latter could serve as proxies for the former. This would be ironic, as it would then allow macrofaunal diversity patterns to be measured by macrofaunal abundance patterns! Such an approach would greatly simplify analysis of community structure, however (and was in fact done to some extent by the author).

Organic matter supply has been seen to influence macrofaunal diversity both directly and indirectly. Direct influence includes aggregation of macrofaunal populations around patchy nutrient sources. In deep-sea regions where nutrient supply to the benthos is high (i.e submarine canyons, shallow slope depths), diversity can be retarded. Levin et al. (2001) listed four causes attributable to this.

(1) Takeover by opportunistic species.

(2) Enhanced competitive exclusion.

(3) Increased variability in productivity.

(4) Increased oxygen demand resulting in hypoxia

Environments where high organic matter imports would directly reduce macrofaunal diversity are considered rare, however, particularly as one moves away into deeper waters. Conversely, if food supply is highly reduced (i.e. abyssal plain sites), diversity will suffer (in some taxa) due to a lack of adequate reproductive output (Gage and Tyler, 1991). From a purely trophic consumption standpoint then, macrofaunal diversity is expected to fare the best at intermediate values.

Disturbance theory has not confined itself to directly cueing macrofaunal food supply to diversity, however. A great deal of research has focused upon the role of sediment mixing. This is split into two main branches; sediment mixing as a macrofaunal perturbation force (i.e. burial, predation), and sediment mixing as a trophic partitioning force (creating patches of nutrients). The first (macrofaunal perturbation) is a partial return back to the original megafaunal grazing aspects of disturbance theory. Increased sediment mixing (caused primarily by megafaunal burrowing) not only facilitates direct predation upon macrofauna (Iken et al., 2001), but acts to physically alter the micro-scale habitat in which the macrofauna individually live. In the case of mound building megafauna (i.e. echiuran worms, molpadiid holothuroids), this can result in diversity-reducing burial (Smith et al., 1986).

Bioturbation as a nutrient-partitioning force has been closely studied by Aller and Aller (1986) and Hughes et al. (2005), and thought to account for a great deal of small-scale macrofaunal community variation (Gage, 1997). Pockets of ephemeral organic material derived from deeper sediment layers, detritus-filled burrows, or directly

expelled megafaunal fecal matter (Kukert and Smith, 1992), create uneven macrofaunal distributions both infaunally and epifaunally.

Although the author's only direct diversity measurement ("metadiversity") did not show any strong correlations to support disturbance (or any other) theory, other test variables did. The numerous relationships observed in relation to POC argue for strong trophic controls in the deep Gulf of Mexico. High levels of bioturbation activity and macrofaunal abundances (particularly total fauna, polychaetes and motile crustaceans) displayed discernible relationships with POC, as they would if the community was not at carrying capacity. The sharp drop in abundance and community dominance of sedentary faunas (sponges, strobilas, bivalves, scaphopods) below the 500 m contour may be related to increasing levels of bioturbation, which favor deposit-feeding macrofauna and a late-successional soft sediment community which motile crustaceans appear to exploit unusually well. Beta diversity patterns indicated that biological competition processes were not active in the GoM. This favors a disequilibrium model controlling macrofaunal diversity. The high bioturbation intensities measured throughout much of the GoM supports that megafaunal activity must also be high.

4.9.2. Intermediate Disturbance Theory

With the recent developments in deep-sea biology, particularly regarding the better understanding of nutrient imports and its spatial dispersal onto the seafloor, benthic diversity is increasingly believed to be maintained by a dynamic balance of community carrying capacity versus disturbance mechanisms (Gage, 1997). This intermediate

disturbance model is essentially a fusion of disequilibrium and equilibrium processes, but since it ultimately never attains an equilibrium condition, it is categorized as a predominantly disturbance-driven process. As explained in section 1, this theory infers that disturbance events exist but not to the extent where either long-term or large-scale diversity levels are impinged upon. Several recent studies have shown support for intermediate disturbance theory (Paterson and Lambshead, 1995; Aller, 1997; Cartes et al., 2001), but perhaps the best example is by Kukert and Smith (1992). This study is considered one of the best examinations of small-scale macrofaunal diversity maintenance.

4.9.2.1. Kukert and Smith's Artificial Mound Experiments

It was not until the early 1990's that Kukert and Smith (1992) claimed to show the first *direct* evidence for intermediate disturbance in deep-sea macrofauna. Using artificial sediment mounds in the Santa Catalina Basin as a test environment, they intermittently monitored (over a 23 month period) the occurrence of various macrofaunal trophic, domicile, and mobility groups. Kukert and Smith found that in comparison to adjacent background sediments, the communities within the artificial mounds exhibited rapid population growth (following a 60-70% species richness decline after being initially buried), and after 23 months, heightened diversity over non-mound samples. Faunal abundances for simple mound treatments reached two-thirds the level of non-mound background sites within three months, and equal abundance values were reached after 11 months. Artificial mounds possessing PVC "floors" had much slower

colonization rates. Kukert and Smith inferred from their experiment that macrofauna were highly resistant to burial, and that in the event of such occurrences, repopulation of overlying sediments could occur rapidly from infaunal burrowing forms. Their “direct support” for intermediate disturbance processes was the enhanced species diversity observed in late-successional mounds, which Kukert and Smith believed to not be a result of habitat partitioning within the mounds (which at 23 months were visually indistinguishable from the background surface), but reduced competitive pressures from normally dominant species (which suffered disproportional abundance losses during mound treatments).

4.10. Difficulties in Using Higher Order Taxonomy

In recent years, investigations have mounted into the efficacy of substituting species-level identifications with higher level taxa. This has primarily been the result of two significant changes that have complicated macrofaunal community studies, the increasing rarity of specialist taxonomists required for high-level identifications, and the rising costs associated with basic faunal extractions and rough identifications. The latter concern is primarily economic, related to the increasing per-person costs involved with funding large numbers of laboratory personnel, and is not discussed further. However, the other concern (trained taxonomists) is the responsibility of the scientific community, and in fact is considered to be much more serious.

4.10.1. The Taxonomic Impediment, and Taxonomic Sufficiency

Since the late 1970's and early 1980's, there has been a rapidly dwindling number of trained taxonomists capable of performing lower-order specimen identifications, not just for the deep-sea, but for most habitats and living groups. Referred to as the "taxonomic impediment" in a review by Giangrande (2003), the progressive decline of taxonomists throughout Europe and the United States (where most ecological science is performed) has impeded if not stifled ecosystem-based research. Giangrande points out that in order for ecologists to fully understand the biological interactions taking place within a habitat, knowledge of individual species is often required. Yet a systematist is usually required at some point to properly identify and describe such species. Historically, where ecologists could not acquire the systematists they needed, these ecologists would train themselves to a level deemed sufficient for their own research. This has been particularly true in deep-sea macrofaunal and meiofaunal work, as evidenced by the narrow (and repetitive) taxonomic focus of most studies. While this practice of "parataxonomy" was generally deemed sufficient up through the 1980's, the retirements and/or deaths of taxonomists without replacement since then have significantly curtailed the primary mechanism for cross-training ecologists. This has resulted in situations where it is now a common occurrence for marine macrofaunal surveys to not identify half or more of their collected species because they are unable to do so (Maurer, 2000). Wicksten (personal communication) observes that for many higher-order invertebrate groups, the number of specialist taxonomists for them (worldwide) is limited to two or three individuals, most

of whom are elderly and at least partially retired. For some taxa, all known specialists are in fact deceased!

This problem has become so pervasive, particularly within marine invertebrate groups, that Ellis (1985) began to formalize the concept known as “taxonomic sufficiency”. This principle centers around the idea of identifying taxa to the highest ranking possible capable of retaining statistically significant vigor for a particular program’s test hypotheses. It is a cost-benefit approach that realizes that even if genus/species-level identification is possible in a sampling design, the contemporary costs of such an analysis in both time and money will likely prohibit its incorporation (Giangrande, 2003).

Despite the enormous economic appeal of taxonomic sufficiency, its usage over the last twenty years has largely remained limited to pollution studies and government-sponsored environmental monitoring programs. The reason for this is not well-established, but probably is largely due with the original premise that the technique be confined to heavily damaged ecosystems capable of altering community diversity sufficiently to be reliably measured at higher taxonomic levels (Warwick and Clarke, 1993). Typically, taxonomic sufficiency is practiced at no higher than the family level, as comparative studies against the genus and species-levels with test variables have shown it to correlate well (if more weakly than genus and species-level). It has seen very limited use in deep-sea studies. Two of these are briefly mentioned.

Touting itself as the first study was Bhayani et al. (2003), which entailed comparing the usefulness of polychaetes sorted to family-level vs. those sorted to species, in the

outer shelf and upper slope waters of the Faroe-Shetland Channel (NE Atlantic). The results of the experiment indicated that family-level discrimination was markedly inferior to species-level, and that any time and expense-saving advantages to using family-level taxonomy in highly disturbed sediment communities would be better spent using faunal abundance or biomass counts instead.

Coming out the same year (and actually preceding it by two months) was a report by Doerries and Van Dover (2003) of the taxonomic sufficiency method within deep chemosynthetic communities. They reported high correlations of taxonomic levels all the way to order-level, and recommended use of the taxonomic sufficiency approach for large-scale areal surveys. It should be noted however that chemosynthetic communities, despite being “deep-sea environments”, have a radically different community structure comprising very low species diversity (Van Dover, 2003). The species:genus (and even species:family!) ratios are often 1:1, and the species:order ratio 2:1 (Doerries and Van Dover, 2003). Thus, correlating ecological variables with a particular chemosynthetic species is likely to be identical to that using a family-level classification, because in the case of the latter only one species is still represented!

More “extreme” higher-taxonomic identifications similar to that partially used by the author (phylum-level) are less common that that using genus or family-level, and primarily follow the work of Warwick and Clarke (1993). Generally, such studies are confined to shallow-water, polluted estuaries or bays (Drake et al., 1999; Muniz and Pires-Vanin, 2005), but Olsgard et al. (1998) sampled within the shelf waters of the North Sea down to depths of 380 m. In all of these papers, the phylum-level approach

either did not correlate to any test factors, or the correlations were found to be much weaker than that of lower taxonomic levels (i.e. family).

The author's adaptation of rough faunal lists into a diversity measurement proved to be of little practical utility. As such, the author confirms the opinions of workers like Warwick (1988), Olsgard et al. (1998), and Gage (2001) that in natural ecosystems not significantly perturbed by human activity, the taxonomic sufficiency approach should not be applied. Rather, classical genus/species identifications should be maintained (i.e. Thistle, 1983) or alternative functional or trophic group identifications (i.e. Muniz and Pires-Vanin, 2005; Stora et al., 1999) be used.

Gage (2001) uses examples of taxonomic sufficiency techniques applied in shallow water pollution studies to bolster the importance of lower-order faunal identifications. Gage states "…as stress increases, the adaptability of first individuals, then the species, and then genus, family and so on, is exceeded, so that increasing stress is manifest at progressively higher taxonomic levels." From this, Gage wished to be made clear that lower levels of test specimen identifications should result in greater measurement sensitivity of ecological responses than identifications of organisms to higher taxonomic levels. From this dissertation's almost total lack of test correlations using such a higher taxonomic approach (and not a single significant regressional relationship), the author is inclined to agree with Gage. Due to the many difficulties involved with deep-sea sampling and the number of indirect and proxy measurements already in use to examine community structure, it would seem a prudent decision to not further dilute our ability to

measure macrofaunal ecological interactions by simplifying the way we delineate discrete populations.

4.11. Test Factors Not Included in This Study

4.11.1. Other Trophic Measurements

Bottom-water POC was our primary test measurement for macrofaunal food supply, and sediment TOC was later added as a second trophic variable. Other measures (DOC, nitrate, sea surface primary productivity, benthic sargassum) were also initially considered, but quickly ruled out for various reasons. Sediment DOC and nitrate were placed in the same correlation matrix as bottom-water POC, and found to either lack significant correlations to other test factors, or measure correlations that were unsupported by regression testing. Sea surface primary productivity was thought to be too distance-decoupled for use as a local-scale measurement (DGoMB stations were separated from immediately overlying surface waters by 1,600 m on average). Presence of benthic sargassum was noted by Ziegler (2002) from DGoMB photographs. "Accumulation" regions were reported throughout large areas in the eastern, central and western GoM, and an attempt was made to quantify density based on numerical counts of "clumps" seen in photographs. Ziegler reported higher densities in the western GoM than in the eastern GoM. Sargassum was also recorded from DGoMB megafaunal trawls, either directly or removed from the gut of the common paxillosid asteroid *Dytaster*. Sargassum was not evaluated in this study due to time constraints (requiring a complete reexamination of seafloor photographs).

4.11.2. Trawled Megafauna as Sediment Disturbance Indicators

Attempts to determine local-scale habitat relief using trawled megafauna as indicator species was not successful. Although many DGoMB trawls yielded a wide variety of faunas known to prefer both low-disturbed sediments (solitary corals, sponges, anemones) as well as genera known to burrow extensively (*Chaceon*, *Bathynomus*, *Molpadia*, *Brissopsis*), only rarely could discrete patterns be noticed. Many trawls contained both heavy-burrowing *and* anchored sedentary forms in large quantities. Inconclusive results such as those could be interpreted to indicate multiple *megafauna-scale* microhabitats within a local area, or that biological competition for benthic habitat is unimportant. It is difficult to imagine, for instance a local-scale, deep-sea habitat where solitary corals and large burrowing crabs coexist, yet this appears to be the case at station S42 on the Florida Escarpment.

5. SUMMARY REMARKS

The DGoMB project was originally designed to measure regional community structure and function within the Gulf of Mexico, *not* examine local-scale patterns. However, the sheer amount of data generated from the project enabled the author to adapt certain measurements and analysis techniques for use towards local-scale examination. Furthermore, some of these analytical methodologies (i.e. turnover diversity, abundance patchiness) could be used to explore regional-scale processes in ways different from those of the original DGoMB design.

Worldwide, the majority of deep-sea macrofaunal studies comprise only a few sites at one time, or one to a few sites measured multiple times. While this may permit more detailed examination of the biota and environment at the local-scale, biologists are hesitant to make generalizations about their findings towards the rest of the deep sea biome, similar or adjacent habitats, or even the *same* locale at later dates.

This uncertainty is reflected in the deep-sea literature. Ecological patterns and trends are rarely discussed except at very broad (total fauna) or very specific (individual species) levels. Even then, such discussion is often hedged with a great many qualifiers. Even today, there are a surprising amount of predictions and premises that are based on little to no direct measurements. This is confounded by studies which often seek to answer identical questions, yet report conflicting results. This has forced biologists to ask increasingly narrower questions, which yield correspondingly narrower results. The critical decline of trained taxonomists and the dwindling availability of research vessels capable of performing deep-sea research have slowed progress in this discipline to a

trickle. The last major textbook (excluding chemosynthetic communities) was released over 15 years ago; more recent literature reviews (i.e. Levin et al., 2001) are few and often highly limited in scope. It is ironic and tragic that with the current public perception and popularity towards "biodiversity" and marine biology, our ability to study the deep-sea environment is far more handicapped than it was twenty or even thirty years ago. Rather than physically collect samples, we often make do with photographs. Instead of classifying organisms to lowest available taxon, we modify our test hypotheses to accommodate far broader taxonomic resolutions. Weeks of shipboard time have now been reduced to days.

All of these issues only exemplify the importance and usefulness of the DGoMB project. It is one of only a handful of deepwater studies that have *ever* examined deepwater benthic communities at multiple faunal scales and over a large number of sites, and the *only one* which has sampled a large enough spatial area to attempt to model the ecosystem at a basin-wide scale. The wide variety of types and the large amount of biological, chemical, physical, and geological measurements is sufficient to not only sustain a great many present and future studies by itself, but the raw data is publicly available in electronic format. This will enormously facilitate inter-studies comparisons and hopefully permit an integration of research work that is desperately needed. Finally, the vast quantity of macrofaunal specimens is available for taxonomists to work up, and in fact have begun to be analyzed (albeit mostly limited to one boxcore sample per survey site).

In the case of the author's interest to explore prominent deep-sea biodiversity theories, two DGoMB raw data components (seafloor photographs and boxcore macrofaunal counts) were selected out and analyzed in a manner thought suitable for hypothesis testing. Combined with other raw measurements (i.e. sediment grain fractions, POC) that were not modified by the author, it was hoped that ecological patterns and/or driving forces could be identified to either support or refute test hypotheses. Although the study was hindered by aspects of the DGoMB sampling program that could not be fully modified to the author's study (i.e. more than one sediment chemistry measurement per station), or were much broader than was hoped (i.e. taxonomic resolution), other design components (i.e. faunal abundances, number of within-site boxcores) fit very well.

Although not explicitly envisioned by the author as such, this study was in many respects much more exploratory in nature than in clarifying specific test hypotheses. Although many significant ecological correlations were found, and to a (much) lesser extent significant relationships that supported/refuted test hypotheses, a great deal of experience was accrued on how to make improvements on or increase the scope of the study. Additionally, other DGoMB collaborators' recent publications, as well as the upcoming release of the final program report, have made available additional or better refined data, and a great deal of professional analyses and interpretations.

The author intends to use the information obtained from this study and other DGoMB-related research to create more refined hypothesis tests (i.e. examine correlations with specific macrofaunal taxa, use more versatile statistical testing), and

possibly examine other ecological questions not originally designed for (i.e. importance of bottom currents, integrate non-DGoMB data). Taking existing biological measurements and subdividing them into narrower, more discrete subunits, and incorporating additional environmental test factors, sample sites, and even sample *times*, should enable improvements in isolating ecological controlling factors, and community effects as a result of such factors.

Just as data from the North Atlantic Slope and Rise study carried out in the mid-1980's continues to be studied even today, data from the DGoMB project will serve as a valuable research resource for many years to come.

REFERENCES

Abele, L.G., Walters, K., 1979. Marine benthic diversity: a critique and alternative parameters. Journal of Biogeography, 6, 115-126.

Allen, J.A., Sanders, H.L.,1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: the epilogue. Progress in Oceanography, 38 (2), 95-153.

Aller, J.Y., 1997. Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region. Deep-Sea Research I, 44, 39-69.

Aller, J.Y., Aller, R.C., 1986. Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. Deep-Sea Research, 33(6), 755-790.

Balsam, W.L., Payne Beeson, J., 2003. Sea-floor sediment distribution in the Gulf of Mexico. Deep-Sea Research I, 50, 1421-1444.

Blankenship, L.E., Yayanos, A.A., Cadien, D.B., Levin, L.A., 2006. Vertical zonation patterns of scavenging amphipods from the Hadal zone of the Tonga and Kermadec Trenches, Deep-Sea Research I, 53, 48-61.

Borowski, C., Thiel, H., 1998. Deep-sea macrofaunal impacts of a large-scale physical disturbance experiment in the Southeast Pacific. Deep-Sea Research II, 45, 55-81.

Carney, R.S., 1997. Basing conservation policies for the deep-sea floor on current-diversity concepts: a consideration of rarity. Biodiversity and Conservation, 6, 1463-1485.

Carney, R.S., 2001. Management applicability of contemporary deep-sea ecology and reevaluation of Gulf of Mexico studies. final report. OCS Study MMS2001-095. U.S. Department of the Interior Minerals Management Service, Gulf of Mexico OCS Region Office, New Orleans, LA. 174 pp.

Cartes, J.E., Elizalde, M., Sorbe, J.C., 2001. Contrasting life-histories, secondary production, and trophic structure of Peracarid assemblages of the bathyal suprabenthos from the Bay of Biscay (NE Atlantic) and the Catalan Sea (NW Mediterranean). Deep-Sea Research I, 48, 2209-2232.

Cartes, J.E., Sorbet, J.C., 1996. Temporal population structure of deep-water cumaceans from the western Mediterranean slope. Deep-Sea Research I, 43(9), 1423-1438.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science, 199, 1302-1309.

Cosson, N., Sibuet, M., Galeron, J., 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. Deep-Sea Research I, 44(2), 247-269.

Dayton, P.K., Hessler, R.R., 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Research, 19, 199-208.

Diaz, R. J., 2004. Biological and physical processes structuring deep-sea surface sediments in the Scotia and Weddell Seas, Antarctica. Deep-Sea Research II, 51, 1515-1532.

Doerries, M.B., Van Dover, C.L., 2003. Higher-taxon richness as a surrogate for species richness in chemosynthetic communities. Deep-Sea Research I, 50, 749-755.

Drake, P., Baldo, F., Saenz, V., Arias, A.M., 1999. Macrobenthic community structure in estuarine pollution assessment on the Gulf of Cadiz (SW Spain): is the phylum-level meta-analysis approach applicable? Marine Pollution Bulletin, 38(11), 1038-1047.

Dytham, C., 1999. Choosing and using statistics: a biologist's guide. Blackwell Science, USA, 218 pp.

Ellis, D., 1985. Taxonomic sufficiency in pollution assessment. Marine Pollution Bulletin, 16, 459.

Etter, R.J., Grassle, J.F., 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature, 360, 576-578.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology: an Annual Review, 17, 193-284.

Gage, J.D., 1997. High benthic species diversity in deep-sea sediments: The importance of hydrodynamics. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: patterns and processes, Cambridge University Press, Cambridge, 148-177.

Gage, J.D., 2001. Deep-sea benthic community and environmental impact assessment at the Atlantic Frontier. Continental Shelf Research, 21, 957-986.

Gage, J.D., Tyler, P.A., 1991. Deep-Sea Biology: A natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, 504 pp.

Gallaway, B.J., Martin, L.R., Howard, R.L., (Eds.), 1988. Northern Gulf of Mexico continental slopes study, annual report: Year 3. volume I: executive summary. Annual report submitted to the Minerals Management Service, New Orleans, LA. Contract No. 14-12-0001-30212. OCS Study/MMS 87-0059, 141 pp.

Gallaway, B.J., (Ed.), 1988. Northern Gulf of Mexico continental slope study, annual report: year 4. volume I: executive summary. Annual report submitted to the Minerals Management Service, New Orleans, LA. Contract No. 14-12-0001-30212. OCS Study/MMS 88-0052, 69 pp.

Garrison, L.E., Martin, Jr., R.G., 1973. Geologic structures in the Gulf of Mexico basin. U.S. Geological Survey Professional Paper, 773. U.S. Government Printing Office, Washington D.C., 85 pp.

Giangrande, A., 2003. Biodiversity, conservation, and the “taxonomic impediment”. Aquatic Conservation: Marine and Freshwater Ecosystems, 13, 451-459.

Glover, A., Paterson, G., Bett, B., Gage, J., Sibuet, M., Sheader, M., Hawkins, L., 2001. Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain. Deep-Sea Research I, 48, 217-236.

Gordon, D.C., 1970. Some studies on the distribution and composition of particulate organic carbon in the North Atlantic Ocean. Deep-Sea Research, 17, 233-243.

Grassle, J.F., Maciolek, N.J., 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. American Naturalist, 139, 313-341.

Grassle, J.F., Morse-Porteous, L.S., 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-Sea Research, 34, 1911-1950.

Grassle, J.F., Sanders, H.L., 1973. Life histories and the role of disturbance. Deep-Sea Research, 20, 643-659.

Grassle, J.F, Smith, W., 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. Oecologia, 25, 13-22.

Gray, J.S., 1974. Animal-sediment relationships. Oceanography and Marine Biology. An Annual Review, 12, 223-261.

Gray, J.S., 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. Journal of Experimental Marine Biology and Ecology, 250, 23-49.

Hogue, E.W., Miller, C.B., 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. Journal of Experimental Marine Biology and Ecology, 53, 181-191.

Heezen, B.C., Hollister, C.D., 1971. The face of the deep. Oxford University Press, New York, 659 pp.

Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep-sea. Deep-Sea Research, 14, 65-78.

Hessler, R.R., Jumars, P.A., 1974. Abyssal community analysis from replicate box cores in the central North Pacific. Deep-Sea Research, 21, 185-209.

Hughes, D.J., Brown, L., Cook, G.T., Cowie, G., Gage, J.D., Good, E., Kennedy, H., MacKenzie, A.B., Papadimitriou, S., Shimmield, G.B., Thomson, J., Williams, M., 2005. The effects of megafaunal burrows on radiotracer profiles and organic composition in deep-sea sediments: preliminary results from two sites in the bathyal north-east Atlantic. Deep-Sea Research I, 52, 1-15.

Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography, 50, 383-405.

Ingole, B.S., Ansari, Z.A., Rathod, V., Rodriguez, N., 2001. Response of deep-sea macrobenthos to a small-scale environmental disturbance. Deep-Sea Research II, 48, 3401-3410.

Ivany, L.C., Newton, C.R., Mullins, H.T., 1994. Benthic invertebrates of a modern carbonate ramp: A preliminary survey. Journal of Paleontology, 68(3), 417-433.

Jumars, P.A., 1975. Environmental grain and polychaete species diversity in a bathyal benthic community. Marine Biology, 30, 253-266.

Jumars, P.A., Eckman, J.E., 1983. Spatial structure within deep-sea benthic communities. In: Rowe, G.T. (Ed.) The Sea, vol. 8, John Wiley & Sons, Inc., New York, 399-451.

Jumars, P.A., Gallagher, E.D., 1982. Deep-sea community structure: three plays on the benthic proscenium. In: Ernst, W.G. and Morin, J.G. (Eds.) The Environment of the Deep Sea, Prentice-Hall, Inc., New Jersey, 217-285.

Kaim-Malka, R.A., 1998. Biology and life cycle of *Natatolana borealis* Lilj. 1851, a scavenging isopod from the continental slope of the Mediterannean. Deep-Sea Research I, 44(12), 2045-2067.

Kaufman, R.S., Smith, J.R., 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: results from a 17-month time-lapse photographic study. Deep-Sea Research I, 44(4), 559-579.

Kaser, R.T., Cox, V.C., 1999. Metadiversity: The grand challenge for biodiversity information management through metadata: the call for community: proceedings of the symposium sponsored by U.S. Geological Survey, Biological Resources Division and the National Federation of Abstracting and Information Services. National Federation of Abstracting and Information Services, Philadelphia, USA.

Kropp, R.K., 2004. Review of deep-sea ecology and monitoring as they relate to deep-sea oil and gas operations. Pacific Northwest National Laboratory, Prepared for the U.S. Department of Energy under Contract DE-AC06-76RL01830, 63 pp.

Kukert, H., Smith, C.R., 1992. Disturbance, colonization and succession in a deep-sea sediment community: artificial-mound experiments. Deep-Sea Research, 39, 1349-1371.

Laws, E.A., Archie, J.W., 1981. Appropriate use of regression analysis in marine biology. Marine Biology, 65, 13-16.

Levin, L.A., Gage, J.D., 1998. Relationships between oxygen, organic matter, and the diversity of bathyal macrofauna. Deep-Sea Research II, 45, 129-163.

Levin, L.A., Smith, C.R., 1984. Response of background fauna to disturbance and enrichment in the deep sea: a sediment tray approach. Deep-Sea Research, 31(11), 1277-1285.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annual Review of Ecology and. Systematics, 32, 51-93.

Lauerman, L.M.L., Kaufman, R.S., Smith, K.L., 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I, 43(7), 1075-1103.

Macdonald, A.G., 1975. Physiological aspects of deep sea biology. Cambridge University Press, Cambridge, London, 450 pp.

Marshall, N.B., 1954. Aspects of deep sea biology. Hutchinson, London. 380 pp.

Marshall, N.B., 1979. Developments in deep-sea biology. Blandford Press, UK. 566 pp.

Maurer, D., 2000. The dark side of taxonomic sufficiency (TS). Marine Pollution Bulletin, 40(2), 98-101.

Morse, J.W., Beazley, M.J., in review. Organic matter in deep water sediments of the Northern Gulf of Mexico and its relationship to the distribution of benthic organisms. Texas A&M University.

Mullineaux, L.S., 1989. Vertical distributions of the epifauna on manganese nodules: implications for settlement and feeding. Limnology and Oceanography, 34(7), 1247-1262.

Muniz, G.P., Pires-Vanin, A.M.S., 2005. More about taxonomic sufficiency: a case study using polychaete communities in a subtropical bay moderately affected by urban sewage. Ocean Science Journal, 40(3), 127-143.

Narayanaswamy, B.E., Nickell, T.D., Gage, J.D., 2003. Appropriate levels of taxonomic discrimination in deep-sea studies: species vs family. Marine Ecology Progress Series, 257, 59-68.

Olsgard, F., Somerfield, P.J., Carr, M.R., 1998. Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. Marine ecology progress series, 172(25), 25-36.

Osman R.W., Whitlatch, R.B., 1978. Patterns of species diversity: fact or artifacts? Paleobiology, 4, 41-54.

Paterson, G.L.J., Lambshead, P.J.D., 1995. Bathymetric patterns of polychaete diversity in the Rockall Trough, northeast Atlantic. Deep-Sea Research I, 42(7), 1199-1214.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology. An Annual Review, 16, 229-311.

Pequegnat, W.E., 1983. The ecological communities of the continental slope and adjacent regimes of the northern Gulf of Mexico. Prepared for the Minerals Management Service by TerEco Corp. Contract No. AA851-CT1-12, 384 pp.

Pequegnat, W.E., Gallaway, B.J., Pequegnat, L.H., 1990. Aspects of the ecology of the deep-water fauna of the Gulf of Mexico. American Zoologist, 30, 45-64.

Pineda, J., 1993. Boundary effects on the vertical ranges of deep-sea benthic species. Deep-Sea Research I, 40, 2179-2192.

Rex, M.A., Etter, R.J., Stuart, C.T., 1997. Large-scale patterns of species diversity in the deep-sea benthos. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: patterns and processes, Cambridge University Press, Cambridge, 94-121.

Rex, M.A., Crame, J.A., Stuart, C.T., Clarke, A., 2005. Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity. Ecology, 86(9), 2288-2297.

Riley, G.A., 1970. Particulate and organic matter in sea water. Advances in marine biology, 8, 1-118.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research, 28, 150-178.

Rhoads, D.C., 1974. Organism-sediment relations on the muddy sea floor. Oceanography and Marine Biology. An Annual Review, 12, 263-300.

Rowe, G.T., in review. DGOMB final program report. Texas A&M University.

Sanders, H.L., 1968. Marine benthic diversity: a comparative study. American Naturalist, 102, 243-282.

Schaff., T.R., Levin, L.A.,1994. Spatial heterogeneity of benthos associated with biogenic structures on the North Carolina continental slope. Deep-Sea Research II, 41, 901-918.

Slobodkin, L.B., Sanders, H.L., 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol., 22, 82-92.

Smith, C.R., 1986. Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep sea. Journal of Marine Research, 44, 567-600.

Smith, C.R., 1994. Tempo and mode in deep-sea benthic ecology: punctuated equilibrium revisited. Palaios, 9, 3-13.

Smith, C.R., Jumars, P.A., DeMaster, D.J., 1986. *In situ* studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. Nature, 323, 251-253.

Smith, K.L., Kaufman, R.S., Wakefield, W.W., 1993. Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep-Sea Research I, 40(11/12), 2307-2324.

Smith, C.R., Rabouille, C., 2002. What controls the mixed-layer depth in deep-sea sediments? The importance of POC flux. Limnology and Oceanography, 47, 418-426.

Snelgrove, P.V.R., Grassle, J.F., Petrecca, R.F., 1996. Experimental evidence for aging food patches as a factor contributing to high deep-sea macrofaunal diversity. Limnology and Oceanography, 41, 605-614.

Sokolova, M.N., 1972. Trophic structure of deep-sea macrobenthos. Marine Biology, 16, 1-12.

Soltwedel T., Queric, N., Vopel, K., 2002. Effects of micro-scale environmental heterogeneity on small sediment-inhabiting organisms. Reports on Polar and Marine Research, 422, 11-20.

Stora, G., Bourcier, M., Arnoux, A., Gerino, M., Le Campion, J., Gilbert, F., Durbec, J., 1999. The deep-sea macrobenthos on the continental slope of the northwestern Mediterranean Sea: a quantitative approach. Deep-Sea Research I, 46, 1339-1368.

Thistle, D., 1983. The role of habitat heterogeneity in deep-sea diversity maintenance. Deep-Sea Research, 30A, 1235-1245.

Thistle, D., Wilson, G.D.F., 1996. Is the HEBBLE isopod fauna hydrodynamically modified: A second test. Deep-Sea Research I, 43(4), 545-554.

Tselepides, A., Lampadariou, N., 2004. Deep-Sea meiofaunal community structure in the eastern Mediterranean: are trenches benthic hotspots? Deep-Sea Research I, 51, 833- 847.

Turekian, K. K., Cochran, J. K., Kharkar, D. P., Cerrato, R. M., Vaisnys, J. R., Sanders, H. L., Grassle, J. F, Allen, J. A., 1975. Slow growth rate of a deep-sea clam determined by ^{228}Ra chronology. Proceedings of the National Academy of Sciences of the USA, 72, 2829-2832.

Uchupi, E., 1975. Physiography of the Gulf of Mexico and Caribbean Sea. In: Nairn, A.E.M., Stehli, F.G. (Eds.), The Ocean Basins and Margins, Vol. 3, The Gulf of Mexico and the Caribbean, Plenum Press, New York, 1-64.

Valiela, I., 1995. Marine ecological processes, 2nd edition. Springer-Verlag New York Inc., USA, 686 pp.

Valentine, J.W., 1973. Evolutionary paleoecology of the marine biosphere. Prentice-Hall, New Jersey.

Van Dover, C.L., 2003. The ecology of deep-sea hydrothermal vents. Princeton University Press, New Jersey, 424 pp..

Vetter, E.W., Dayton, P.K., 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep-Sea Research II, 45, 25-54.

Warwick, R.M., 1988. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. Marine Pollution Bulletin, 6, 259-268.

Warwick, R.M., Clarke, K.R., 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. Marine Ecology Progress Series, 92, 221-231.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains. Oregon and California. Ecol. Monogr., 30, 279-338.

Wilson, M.V., Schmida, A., 1984. Measuring beta diversity with presence and absence data. J. Ecol., 72, 1055-1064.

Ziegler, M.P., 2002. The epibenthic megafauna of the northern Gulf of Mexico continental slope. Master's Thesis, Texas A&M University, College Station, Texas, unpublished.

APPENDIX A

RESULTS OF CORRELATION ANALYSIS TO TEST VARIABLES

	Kendall's tau-b	water depth	bioturbation	%sand	%silt	%clay	POC	LOG POC
water depth	Correl. Coefficient	1.000	-.427(**)	-0.154	0.111	0.123	-.552(**)	-.552(**)
	Sig. (2-tailed)	.	0.002	0.227	0.380	0.329	0.000	0.000
bioturbation	Correl. Coefficient	-.427(**)	1.000	0.084	0.148	-0.168	.329(*)	.329(*)
	Sig. (2-tailed)	0.002	.	0.543	0.282	0.220	0.016	0.016
%sand	Correl. Coefficient	-0.154	0.084	1.000	-.338(**)	-.522(**)	.255(*)	.255(*)
	Sig. (2-tailed)	0.227	0.543	.	0.009	0.000	0.048	0.048
%silt	Correl. Coefficient	0.111	0.148	-.338(**)	1.000	-0.186	-0.083	-0.083
	Sig. (2-tailed)	0.380	0.282	0.009	.	0.147	0.514	0.514
%clay	Correl. Coefficient	0.123	-0.168	-.522(**)	-0.186	1.000	-.324(*)	-.324(*)
	Sig. (2-tailed)	0.329	0.220	0.000	0.147	.	0.011	0.011
POC	Correl. Coefficient	-.552(**)	.329(*)	.255(*)	-0.083	-.324(*)	1.000	1.000(**)
	Sig. (2-tailed)	0.000	0.016	0.048	0.514	0.011	.	.
LOG POC	Correl. Coefficient	-.552(**)	.329(*)	.255(*)	-0.083	-.324(*)	1.000(**)	1.000
	Sig. (2-tailed)	0.000	0.016	0.048	0.514	0.011	.	.
total mean abundance	Correl. Coefficient	-.539(**)	.426(**)	0.106	0.105	-0.158	.501(**)	.501(**)
	Sig. (2-tailed)	0.000	0.002	0.405	0.407	0.211	0.000	0.000
LOG total mean abundance	Correl. Coefficient	-.536(**)	.433(**)	0.107	0.101	-0.154	.511(**)	.511(**)
	Sig. (2-tailed)	0.000	0.001	0.405	0.425	0.222	0.000	0.000
total pooled abundance	Correl. Coefficient	-.539(**)	.426(**)	0.106	0.105	-0.158	.501(**)	.501(**)
	Sig. (2-tailed)	0.000	0.002	0.405	0.407	0.211	0.000	0.000
total mean richness	Correl. Coefficient	-.450(**)	.315(*)	.295(*)	0.037	-.280(*)	.481(**)	.481(**)
	Sig. (2-tailed)	0.000	0.021	0.021	0.770	0.027	0.000	0.000
total pooled richness	Correl. Coefficient	-0.242	0.181	0.185	-0.145	0.004	0.144	0.144
	Sig. (2-tailed)	0.058	0.194	0.158	0.266	0.974	0.266	0.266
metadiversity	Correl. Coefficient	.289(*)	-0.202	0.094	-0.105	0.039	-0.203	-0.203
	Sig. (2-tailed)	0.020	0.135	0.462	0.407	0.757	0.108	0.108
taxonomic beta	Correl. Coefficient	.305(*)	-0.122	-0.194	-0.175	.420(**)	-.464(**)	-.464(**)
	Sig. (2-tailed)	0.014	0.365	0.129	0.167	0.001	0.000	0.000
polychaete u(N)	Correl. Coefficient	-.545(**)	.411(**)	0.146	0.004	-0.184	.524(**)	.524(**)
	Sig. (2-tailed)	0.000	0.002	0.253	0.974	0.143	0.000	0.000
sedentary u(N)	Correl. Coefficient	-.511(**)	0.191	0.148	-0.068	-0.182	.509(**)	.509(**)
	Sig. (2-tailed)	0.000	0.159	0.246	0.591	0.148	0.000	0.000
crustacean u(N)	Correl. Coefficient	-.333(**)	.399(**)	0.019	0.245	-0.092	.431(**)	.431(**)
	Sig. (2-tailed)	0.007	0.003	0.883	0.053	0.464	0.001	0.001
LOG polychaete u(N)	Correl. Coefficient	-.548(**)	.411(**)	0.148	0.002	-0.183	.526(**)	.526(**)
	Sig. (2-tailed)	0.000	0.002	0.246	0.987	0.148	0.000	0.000
LOG sedentary u(N)	Correl. Coefficient	-.514(**)	0.193	0.146	-0.072	-0.177	.514(**)	.514(**)
	Sig. (2-tailed)	0.000	0.154	0.253	0.569	0.162	0.000	0.000
LOG crustacean u(N)	Correl. Coefficient	-.336(**)	.403(**)	0.013	0.243	-0.086	.430(**)	.430(**)
	Sig. (2-tailed)	0.007	0.003	0.922	0.055	0.495	0.001	0.001
polychaete CV	Correl. Coefficient	0.022	0.014	0.231	-0.068	-0.113	0.031	0.031
	Sig. (2-tailed)	0.858	0.920	0.070	0.591	0.371	0.807	0.807
sedentary CV	Correl. Coefficient	-0.143	-0.027	0.185	-0.228	-0.133	0.141	0.141
	Sig. (2-tailed)	0.250	0.840	0.146	0.071	0.291	0.262	0.262
crustacean CV	Correl. Coefficient	0.200	-.290(*)	-0.144	-0.060	0.186	-.309(*)	-.309(*)
	Sig. (2-tailed)	0.108	0.032	0.260	0.637	0.139	0.014	0.014
polychaete dominance	Correl. Coefficient	-.341(**)	0.172	0.198	-0.199	-0.121	0.190	0.190
	Sig. (2-tailed)	0.006	0.202	0.121	0.115	0.337	0.131	0.131
sedentary dominance	Correl. Coefficient	-0.059	-0.236	0.085	-0.236	0.010	0.002	0.002
	Sig. (2-tailed)	0.638	0.081	0.503	0.061	0.935	0.987	0.987
crustacean dominance	Correl. Coefficient	0.127	0.041	-0.031	.290(*)	-0.039	0.018	0.018
	Sig. (2-tailed)	0.307	0.763	0.807	0.022	0.757	0.884	0.884

**.Significant at the 0.01 level (2-tailed); *.Significant at the 0.05 level (2-tailed).

	Kendall's tau-b	total mean abundance	LOG total mean abundance	total pooled abundance	total mean richness	total pooled richness
water depth	Correl. Coefficient	-.539(**)	-.536(**)	-.539(**)	-.450(**)	-0.242
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.058
bioturbation	Correl. Coefficient	.426(**)	.433(**)	.426(**)	.315(*)	0.181
	Sig. (2-tailed)	0.002	0.001	0.002	0.021	0.194
%sand	Correl. Coefficient	0.106	0.107	0.106	.295(*)	0.185
	Sig. (2-tailed)	0.405	0.405	0.405	0.021	0.158
%silt	Correl. Coefficient	0.105	0.101	0.105	0.037	-0.145
	Sig. (2-tailed)	0.407	0.425	0.407	0.770	0.266
%clay	Correl. Coefficient	-0.158	-0.154	-0.158	-.280(*)	0.004
	Sig. (2-tailed)	0.211	0.222	0.211	0.027	0.974
POC	Correl. Coefficient	.501(**)	.511(**)	.501(**)	.481(**)	0.144
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.266
LOG POC	Correl. Coefficient	.501(**)	.511(**)	.501(**)	.481(**)	0.144
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.266
total mean abundance	Correl. Coefficient	1.000	.995(**)	1.000(**)	.582(**)	.269(*)
	Sig. (2-tailed)	.	0.000	.	0.000	0.035
LOG total mean abundance	Correl. Coefficient	.995(**)	1.000	.995(**)	.578(**)	.264(*)
	Sig. (2-tailed)	0.000	.	0.000	0.000	0.040
total pooled abundance	Correl. Coefficient	1.000(**)	.995(**)	1.000	.582(**)	.269(*)
	Sig. (2-tailed)	.	0.000	.	0.000	0.035
total mean richness	Correl. Coefficient	.582(**)	.578(**)	.582(**)	1.000	.495(**)
	Sig. (2-tailed)	0.000	0.000	0.000	.	0.000
total pooled richness	Correl. Coefficient	.269(*)	.264(*)	.269(*)	.495(**)	1.000
	Sig. (2-tailed)	0.035	0.040	0.035	0.000	.
metadiversity	Correl. Coefficient	-0.198	-0.201	-0.198	-.290(*)	-.261(*)
	Sig. (2-tailed)	0.112	0.108	0.112	0.020	0.041
taxonomic beta	Correl. Coefficient	-.407(**)	-.407(**)	-.407(**)	-.383(**)	0.148
	Sig. (2-tailed)	0.001	0.001	0.001	0.002	0.246
polychaete u(N)	Correl. Coefficient	.793(**)	.795(**)	.793(**)	.568(**)	.313(*)
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.014
sedentary u(N)	Correl. Coefficient	.633(**)	.638(**)	.633(**)	.501(**)	0.219
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.087
crustacean u(N)	Correl. Coefficient	.665(**)	.671(**)	.665(**)	.537(**)	.303(*)
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.018
LOG polychaete u(N)	Correl. Coefficient	.792(**)	.794(**)	.792(**)	.571(**)	.316(*)
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.014
LOG sedentary u(N)	Correl. Coefficient	.637(**)	.644(**)	.637(**)	.500(**)	0.218
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.089
LOG crustacean u(N)	Correl. Coefficient	.669(**)	.675(**)	.669(**)	.541(**)	.301(*)
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.019
polychaete CV	Correl. Coefficient	0.073	0.067	0.073	0.225	.261(*)
	Sig. (2-tailed)	0.559	0.592	0.559	0.072	0.041
sedentary CV	Correl. Coefficient	0.028	0.030	0.028	0.047	0.031
	Sig. (2-tailed)	0.820	0.808	0.820	0.709	0.807
crustacean CV	Correl. Coefficient	-.383(**)	-.391(**)	-.383(**)	-.314(*)	-0.157
	Sig. (2-tailed)	0.002	0.002	0.002	0.012	0.221
polychaete dominance	Correl. Coefficient	0.234	0.233	0.234	.330(**)	.298(*)
	Sig. (2-tailed)	0.060	0.062	0.060	0.008	0.020
sedentary dominance	Correl. Coefficient	-0.165	-0.160	-0.165	-0.079	-0.131
	Sig. (2-tailed)	0.184	0.200	0.184	0.527	0.304
crustacean dominance	Correl. Coefficient	-0.044	-0.043	-0.044	0.002	-0.031
	Sig. (2-tailed)	0.721	0.733	0.721	0.987	0.807

**.Significant at the 0.01 level (2-tailed); *.Significant at the 0.05 level (2-tailed).

	Kendall's tau-b	metadiversity	taxonomic beta	polychaete u(N)	sedentary u(N)	crustacean u(N)
water depth	Correl. Coefficient	.289(*)	.305(*)	-.545(**)	-.511(**)	-.333(**)
	Sig. (2-tailed)	0.020	0.014	0.000	0.000	0.007
bioturbation	Correl. Coefficient	-0.202	-0.122	.411(**)	0.191	.399(**)
	Sig. (2-tailed)	0.135	0.365	0.002	0.159	0.003
%sand	Correl. Coefficient	0.094	-0.194	0.146	0.148	0.019
	Sig. (2-tailed)	0.462	0.129	0.253	0.246	0.883
%silt	Correl. Coefficient	-0.105	-0.175	0.004	-0.068	0.245
	Sig. (2-tailed)	0.407	0.167	0.974	0.591	0.053
%clay	Correl. Coefficient	0.039	.420(**)	-0.184	-0.182	-0.092
	Sig. (2-tailed)	0.757	0.001	0.143	0.148	0.464
POC	Correl. Coefficient	-0.203	-.464(**)	.524(**)	.509(**)	.431(**)
	Sig. (2-tailed)	0.108	0.000	0.000	0.000	0.001
LOG POC	Correl. Coefficient	-0.203	-.464(**)	.524(**)	.509(**)	.431(**)
	Sig. (2-tailed)	0.108	0.000	0.000	0.000	0.001
total mean abundance	Correl. Coefficient	-0.198	-.407(**)	.793(**)	.633(**)	.665(**)
	Sig. (2-tailed)	0.112	0.001	0.000	0.000	0.000
LOG total mean abundance	Correl. Coefficient	-0.201	-.407(**)	.795(**)	.638(**)	.671(**)
	Sig. (2-tailed)	0.108	0.001	0.000	0.000	0.000
total pooled abundance	Correl. Coefficient	-0.198	-.407(**)	.793(**)	.633(**)	.665(**)
	Sig. (2-tailed)	0.112	0.001	0.000	0.000	0.000
total mean richness	Correl. Coefficient	-.290(*)	-.383(**)	.568(**)	.501(**)	.537(**)
	Sig. (2-tailed)	0.020	0.002	0.000	0.000	0.000
total pooled richness	Correl. Coefficient	-.261(*)	0.148	.313(*)	0.219	.303(*)
	Sig. (2-tailed)	0.041	0.246	0.014	0.087	0.018
metadiversity	Correl. Coefficient	1.000	0.053	-.245(*)	-0.105	-.255(*)
	Sig. (2-tailed)	.	0.673	0.050	0.399	0.041
taxonomic beta	Correl. Coefficient	0.053	1.000	-.349(**)	-.427(**)	-.323(**)
	Sig. (2-tailed)	0.673	.	0.005	0.001	0.009
polychaete u(N)	Correl. Coefficient	-.245(*)	-.349(**)	1.000	.607(**)	.563(**)
	Sig. (2-tailed)	0.050	0.005	.	0.000	0.000
sedentary u(N)	Correl. Coefficient	-0.105	-.427(**)	.607(**)	1.000	.444(**)
	Sig. (2-tailed)	0.399	0.001	0.000	.	0.000
crustacean u(N)	Correl. Coefficient	-.255(*)	-.323(**)	.563(**)	.444(**)	1.000
	Sig. (2-tailed)	0.041	0.009	0.000	0.000	.
LOG polychaete u(N)	Correl. Coefficient	-0.243	-.352(**)	.999(**)	.606(**)	.562(**)
	Sig. (2-tailed)	0.052	0.005	0.000	0.000	0.000
LOG sedentary u(N)	Correl. Coefficient	-0.111	-.423(**)	.615(**)	.997(**)	.443(**)
	Sig. (2-tailed)	0.372	0.001	0.000	0.000	0.000
LOG crustacean u(N)	Correl. Coefficient	-.255(*)	-.322(**)	.563(**)	.447(**)	.997(**)
	Sig. (2-tailed)	0.041	0.010	0.000	0.000	0.000
polychaete CV	Correl. Coefficient	-0.089	-0.085	0.095	-0.069	0.077
	Sig. (2-tailed)	0.475	0.496	0.446	0.581	0.538
sedentary CV	Correl. Coefficient	0.044	0.113	0.050	0.129	-0.185
	Sig. (2-tailed)	0.721	0.364	0.685	0.299	0.136
crustacean CV	Correl. Coefficient	0.016	.250(*)	-.414(**)	-.403(**)	-.347(**)
	Sig. (2-tailed)	0.897	0.044	0.001	0.001	0.005
polychaete dominance	Correl. Coefficient	-0.206	-0.101	.442(**)	.294(*)	0.077
	Sig. (2-tailed)	0.098	0.417	0.000	0.018	0.538
sedentary dominance	Correl. Coefficient	0.174	-0.040	-0.127	0.202	-.298(*)
	Sig. (2-tailed)	0.163	0.746	0.307	0.105	0.016
crustacean dominance	Correl. Coefficient	-0.174	-0.129	-0.115	-0.129	.290(*)
	Sig. (2-tailed)	0.163	0.299	0.355	0.299	0.020

**.Significant at the 0.01 level (2-tailed); *.Significant at the 0.05 level (2-tailed).

	Kendall's tau-b	LOG polychaete u(N)	LOG sedentary u(N)	LOG crustacean u(N)	polychaete CV	sedentary CV
water depth	Correl. Coefficient	-.548(**)	-.514(**)	-.336(**)	0.022	-0.143
	Sig. (2-tailed)	0.000	0.000	0.007	0.858	0.250
bioturbation	Correl. Coefficient	.411(**)	0.193	.403(**)	0.014	-0.027
	Sig. (2-tailed)	0.002	0.154	0.003	0.920	0.840
%sand	Correl. Coefficient	0.148	0.146	0.013	0.231	0.185
	Sig. (2-tailed)	0.246	0.253	0.922	0.070	0.146
%silt	Correl. Coefficient	0.002	-0.072	0.243	-0.068	-0.228
	Sig. (2-tailed)	0.987	0.569	0.055	0.591	0.071
%clay	Correl. Coefficient	-0.183	-0.177	-0.086	-0.113	-0.133
	Sig. (2-tailed)	0.148	0.162	0.495	0.371	0.291
POC	Correl. Coefficient	.526(**)	.514(**)	.430(**)	0.031	0.141
	Sig. (2-tailed)	0.000	0.000	0.001	0.807	0.262
LOG POC	Correl. Coefficient	.526(**)	.514(**)	.430(**)	0.031	0.141
	Sig. (2-tailed)	0.000	0.000	0.001	0.807	0.262
total mean abundance	Correl. Coefficient	.792(**)	.637(**)	.669(**)	0.073	0.028
	Sig. (2-tailed)	0.000	0.000	0.000	0.559	0.820
LOG total mean abundance	Correl. Coefficient	.794(**)	.644(**)	.675(**)	0.067	0.030
	Sig. (2-tailed)	0.000	0.000	0.000	0.592	0.808
total pooled abundance	Correl. Coefficient	.792(**)	.637(**)	.669(**)	0.073	0.028
	Sig. (2-tailed)	0.000	0.000	0.000	0.559	0.820
total mean richness	Correl. Coefficient	.571(**)	.500(**)	.541(**)	0.225	0.047
	Sig. (2-tailed)	0.000	0.000	0.000	0.072	0.709
total pooled richness	Correl. Coefficient	.316(*)	0.218	.301(*)	.261(*)	0.031
	Sig. (2-tailed)	0.014	0.089	0.019	0.041	0.807
metadiversity	Correl. Coefficient	-0.243	-0.111	-.255(*)	-0.089	0.044
	Sig. (2-tailed)	0.052	0.372	0.041	0.475	0.721
taxonomic beta	Correl. Coefficient	-.352(**)	-.423(**)	-.322(**)	-0.085	0.113
	Sig. (2-tailed)	0.005	0.001	0.010	0.496	0.364
polychaete u(N)	Correl. Coefficient	.999(**)	.615(**)	.563(**)	0.095	0.050
	Sig. (2-tailed)	0.000	0.000	0.000	0.446	0.685
sedentary u(N)	Correl. Coefficient	.606(**)	.997(**)	.447(**)	-0.069	0.129
	Sig. (2-tailed)	0.000	0.000	0.000	0.581	0.299
crustacean u(N)	Correl. Coefficient	.562(**)	.443(**)	.997(**)	0.077	-0.185
	Sig. (2-tailed)	0.000	0.000	0.000	0.538	0.136
LOG polychaete u(N)	Correl. Coefficient	1.000	.614(**)	.561(**)	0.097	0.053
	Sig. (2-tailed)	.	0.000	0.000	0.436	0.673
LOG sedentary u(N)	Correl. Coefficient	.614(**)	1.000	.446(**)	-0.071	0.127
	Sig. (2-tailed)	0.000	.	0.000	0.570	0.307
LOG crustacean u(N)	Correl. Coefficient	.561(**)	.446(**)	1.000	0.075	-0.188
	Sig. (2-tailed)	0.000	0.000	.	0.548	0.131
polychaete CV	Correl. Coefficient	0.097	-0.071	0.075	1.000	-0.149
	Sig. (2-tailed)	0.436	0.570	0.548	.	0.230
sedentary CV	Correl. Coefficient	0.053	0.127	-0.188	-0.149	1.000
	Sig. (2-tailed)	0.673	0.307	0.131	0.230	.
crustacean CV	Correl. Coefficient	-.416(**)	-.406(**)	-.346(**)	0.101	0.097
	Sig. (2-tailed)	0.001	0.001	0.006	0.417	0.436
polychaete dominance	Correl. Coefficient	.444(**)	.297(*)	0.075	0.153	0.190
	Sig. (2-tailed)	0.000	0.017	0.548	0.218	0.127
sedentary dominance	Correl. Coefficient	-0.129	0.200	-.301(*)	-0.190	.379(**)
	Sig. (2-tailed)	0.299	0.108	0.016	0.127	0.002
crustacean dominance	Correl. Coefficient	-0.117	-0.135	.289(*)	-0.069	-.315(*)
	Sig. (2-tailed)	0.347	0.277	0.020	0.581	0.011

**.Significant at the 0.01 level (2-tailed); *.Significant at the 0.05 level (2-tailed).

	Kendall's tau-b	crustacean CV	polychaete dominance	sedentary dominance	crustacean dominance
water depth	Correl. Coefficient	0.200	-.341(**)	-0.059	0.127
	Sig. (2-tailed)	0.108	0.006	0.638	0.307
bioturbation	Correl. Coefficient	-.290(*)	0.172	-0.236	0.041
	Sig. (2-tailed)	0.032	0.202	0.081	0.763
%sand	Correl. Coefficient	-0.144	0.198	0.085	-0.031
	Sig. (2-tailed)	0.260	0.121	0.503	0.807
%silt	Correl. Coefficient	-0.060	-0.199	-0.236	.290(*)
	Sig. (2-tailed)	0.637	0.115	0.061	0.022
%clay	Correl. Coefficient	0.186	-0.121	0.010	-0.039
	Sig. (2-tailed)	0.139	0.337	0.935	0.757
POC	Correl. Coefficient	-.309(*)	0.190	0.002	0.018
	Sig. (2-tailed)	0.014	0.131	0.987	0.884
LOG POC	Correl. Coefficient	-.309(*)	0.190	0.002	0.018
	Sig. (2-tailed)	0.014	0.131	0.987	0.884
total mean abundance	Correl. Coefficient	-.383(**)	0.234	-0.165	-0.044
	Sig. (2-tailed)	0.002	0.060	0.184	0.721
LOG total mean abundance	Correl. Coefficient	-.391(**)	0.233	-0.160	-0.043
	Sig. (2-tailed)	0.002	0.062	0.200	0.733
total pooled abundance	Correl. Coefficient	-.383(**)	0.234	-0.165	-0.044
	Sig. (2-tailed)	0.002	0.060	0.184	0.721
total mean richness	Correl. Coefficient	-.314(*)	.330(**)	-0.079	0.002
	Sig. (2-tailed)	0.012	0.008	0.527	0.987
total pooled richness	Correl. Coefficient	-0.157	.298(*)	-0.131	-0.031
	Sig. (2-tailed)	0.221	0.020	0.304	0.807
metadiversity	Correl. Coefficient	0.016	-0.206	0.174	-0.174
	Sig. (2-tailed)	0.897	0.098	0.163	0.163
taxonomic beta	Correl. Coefficient	.250(*)	-0.101	-0.040	-0.129
	Sig. (2-tailed)	0.044	0.417	0.746	0.299
polychaete u(N)	Correl. Coefficient	-.414(**)	.442(**)	-0.127	-0.115
	Sig. (2-tailed)	0.001	0.000	0.307	0.355
sedentary u(N)	Correl. Coefficient	-.403(**)	.294(*)	0.202	-0.129
	Sig. (2-tailed)	0.001	0.018	0.105	0.299
crustacean u(N)	Correl. Coefficient	-.347(**)	0.077	-.298(*)	.290(*)
	Sig. (2-tailed)	0.005	0.538	0.016	0.020
LOG polychaete u(N)	Correl. Coefficient	-.416(**)	.444(**)	-0.129	-0.117
	Sig. (2-tailed)	0.001	0.000	0.299	0.347
LOG sedentary u(N)	Correl. Coefficient	-.406(**)	.297(*)	0.200	-0.135
	Sig. (2-tailed)	0.001	0.017	0.108	0.277
LOG crustacean u(N)	Correl. Coefficient	-.346(**)	0.075	-.301(*)	.289(*)
	Sig. (2-tailed)	0.006	0.548	0.016	0.020
polychaete CV	Correl. Coefficient	0.101	0.153	-0.190	-0.069
	Sig. (2-tailed)	0.417	0.218	0.127	0.581
sedentary CV	Correl. Coefficient	0.097	0.190	.379(**)	-.315(*)
	Sig. (2-tailed)	0.436	0.127	0.002	0.011
crustacean CV	Correl. Coefficient	1.000	-0.238	0.056	-0.048
	Sig. (2-tailed)	.	0.056	0.650	0.697
polychaete dominance	Correl. Coefficient	-0.238	1.000	0.077	-.254(*)
	Sig. (2-tailed)	0.056	.	0.538	0.041
sedentary dominance	Correl. Coefficient	0.056	0.077	1.000	-.282(*)
	Sig. (2-tailed)	0.650	0.538	.	0.023
crustacean dominance	Correl. Coefficient	-0.048	-.254(*)	-.282(*)	1.000
	Sig. (2-tailed)	0.697	0.041	0.023	.

**.Significant at the 0.01 level (2-tailed); *.Significant at the 0.05 level (2-tailed).

APPENDIX B

TEST MEASUREMENTS USED IN STUDY

station	water depth (m)	bioturbation	% sand	% silt	% clay	% Org-C	POC (uM)	DOC (mM)	nitrate (uM)	total mean abundance*
AC1	2479	3	5	35	60	0.695431	1.9	1.91	17.2	286.4
B1	2255	4	4	37	59	0.620252	3.1	0.82	19.2	875.6
B2	2629	3	4	43	54	0.47249	2.2	0.77	13.6	276.2
B3	2618	2	4	39	58	0.60492	2.6	2.26	20.1	320
C1	336	3	4	35	61	0.99752	4.8	2.18	0.2	1131.4
C4	1463	2	11	36	53	0.73464	4.4	1.92	18.9	1155.2
C7	1072	4	9	38	53	0.81533	3.4	1.34	19.8	1405
C12	2921	2	25	41	35	0.4835	2.5	2.91	22.8	710.4
MT3	987	5	6	42	53	0.025365	3.2	2.23	23.8	2418.6
MT4	1401	4	9	46	46	0.9378	2.6	2.72	19.1	1099.4
MT5	2275	2	64	15	20	0.217421	3.3	2.37	14.5	501.8
MT6	2745	1	38	22	40	_	2.4	3.06	10.9	253
NB2	1530	4	10	33	57	0.615317	3.1	0.94	26	580
NB3	1875	2	11	32	58	0.71031	3.1	1.01	23.4	428.4
NB5	2063	2	4	41	55	0.76222	2.9	1.48	21.4	259
RW1	213	4	8	33	59	0.765489	2.8	1.01	8.1	1622.2
RW2	950	4	7	38	56	1.00806	2.9	1.3	28	729.8
RW3	1329	3	8	31	61	0.65666	2.2	1.43	21.5	528
RW4	1574	3	8	31	61	0.79249	2.5	0.52	16.6	526
RW5	1620	3	8	28	64	0.716042	2.5	1.09	17.9	479.8
S35	663	5	12	31	58	1.96169	7.3	3.57	17.4	1895
S36	1828	3	8	41	51	0.871275	3.5	0.74	20.5	2173
S37	2384	5	8	35	57	1.34944	3.2	2.55	19.6	1091.2
S41	2979	5	21	42	37	0.306549	2.3	3.99	36.4	380.6
S42	767	5	21	31	48	0.459427	4.3	3.22	10.6	813.4
S43	361	4	36	38	26	0.563727	4.1	2.66	12	1298.2
S44	213	4	57	27	16	1.97639	4.7	1.66	5.1	1179
W1	405	4	40	28	32	0.511577	4.4	1.02	20	1276
W3	863	5	18	36	47	0.67049	3.7	1.59	26.6	659.4
W5	2753	3	6	34	60	0.8983	2.2	4.23	18.6	273.8
W6	3146	1	14	25	61	0.428089	1.7	0.39	16.5	325.2
WC12	1166	4	11	40	49	0.80052	3.6	1.92	27.4	674.8

*.Values per 0.1725 m^2

station	pooled abundance**	mean richness	total richness	metadiversity	taxonomic beta	polychaete u(N)*	sedentary u(N)*
AC1	1432	14	27	6.66	1.92857	60	19
B1	4378	19	32	6.95	1.68421	135.6	42.4
B2	1381	16.6	24	7.37	1.44578	56	23.6
B3	1600	16.8	23	6.39	1.36905	49.4	48.2
C1	5657	20	29	6	1.45	313.2	397
C4	5776	24.4	33	5.93	1.35246	275.6	85.2
C7	7025	23.4	31	4.96	1.32479	332.6	58.8
C12	3552	19.8	27	8.34	1.36364	122	54
MT3	12093	20.2	30	5.04	1.48515	515	118
MT4	5497	23	35	5.68	1.52174	337.6	73.2
MT5	2509	20.8	31	6.87	1.49038	145	68
MT6	1265	17.6	29	6.94	1.64773	51.6	16.4
NB2	2900	18.6	27	6.68	1.45161	158	44.4
NB3	2142	18.4	30	8.29	1.63043	113.2	55.6
NB5	1295	16.6	26	6.18	1.56627	50.4	29.8
RW1	8111	21.8	36	6.65	1.65138	462.2	458
RW2	3649	21	30	5.94	1.42857	243.4	53.2
RW3	2640	19.2	33	6.63	1.71875	180.6	42
RW4	2630	18.6	30	7.37	1.6129	104.8	46.2
RW5	2399	18.8	28	8.29	1.48936	109.2	59.6
S35	9475	21.8	32	5.79	1.46789	513	69.4
S36	10865	22.8	30	7.25	1.31579	619.8	103
S37	5456	18.2	28	9.19	1.53846	226.4	50
S41	1903	19.4	30	7	1.54639	100	31.2
S42	4067	23.2	33	6.02	1.42241	229.2	69.6
S43	6491	20.4	26	8.31	1.27451	214.6	386
S44	5895	19.6	26	6.48	1.32653	563.8	273
W1	6380	23.8	32	7.26	1.34454	368	480
W3	3297	22.2	34	5.76	1.53153	145	39.6
W5	1369	13.2	22	6.9	1.66667	67.6	23.4
W6	1626	18.2	34	6.89	1.86813	66.6	37.4
WC12	3374	20.4	29	6.64	1.42157	161.2	37.8

*.Values per 0.1725 m^2; **. Values per 0.8625 m^2

station	crustacean u(N)*	polychaete cv	sedentary cv	crustacean cv	polychaete % dominance	sedentary % dominance	crustacean % dominance
AC1	50	44	101	98	20.95	6.63	17.46
B1	129	56.4	53.69	50.8	15.49	4.84	14.73
B2	53.6	27.46	21.73	34.32	20.28	8.54	19.41
B3	86.6	33.77	34.39	47.43	15.44	15.06	27.06
C1	156.2	41.24	79.71	44.03	27.68	35.11	13.81
C4	254.2	51.35	63.78	43.19	23.86	7.38	22
C7	398.6	52.35	50.81	41.43	23.67	4.19	28.37
C12	201	41.07	48.27	46.03	17.17	7.6	28.29
MT3	691.4	16.91	25.28	36.79	21.29	4.88	28.59
MT4	213.4	54.52	52.35	32.52	30.71	6.66	19.41
MT5	97	45.51	92.23	42.6	28.9	13.55	19.33
MT6	39.2	79.95	43.46	56.28	20.4	6.48	15.49
NB2	144	79.87	50.78	58.1	27.24	7.66	24.83
NB3	95	31.37	82.64	23.91	26.42	12.98	22.18
NB5	70.4	19.67	71.95	75.14	19.46	11.51	27.18
RW1	180.4	24.72	112.48	39.04	28.49	28.26	11.12
RW2	140.4	73.14	36.94	44.1	33.35	7.29	19.24
RW3	68.2	51.22	48	87.21	34.2	7.95	12.92
RW4	108.6	36.22	69.44	70.73	19.92	8.78	20.65
RW5	94.8	28.15	30.54	39.72	22.76	12.42	19.76
S35	432.2	42.34	28.76	25.43	27.07	3.66	22.81
S36	347.8	54.42	35.29	31.82	28.52	4.75	16.01
S37	247.6	33.46	49.8	28.79	20.75	4.58	22.69
S41	81.2	46.92	67.06	39.37	26.27	8.2	21.33
S42	198.4	53.02	50.89	29.12	28.18	8.56	24.39
S43	123.4	45.17	73.81	55.8	16.53	29.75	9.51
S44	62	36.4	123.56	17.03	47.82	23.19	5.26
W1	110.4	46.19	84.56	40.75	28.84	37.62	8.65
W3	166.4	37.41	58.15	54.11	21.99	6.01	25.24
W5	41.8	22.03	79.07	110.99	24.69	8.55	15.27
W6	63.8	68.21	47.93	51.24	20.48	11.5	19.62
WC12	168.2	61.79	47.08	46.21	23.89	5.6	24.93

*.Values per 0.1725 m^2

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